
100 MILLION YEARS OF LAND VERTEBRATE EVOLUTION: THE CRETACEOUS-EARLY TERTIARY TRANSITION¹

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ABSTRACT

A critical time interval for vertebrate evolution—between 100 and 112 million years in duration—spans the beginning of the Cretaceous period to the late Eocene epoch of the Cenozoic. This interval encompasses the appearance in the Cretaceous of many of the modern vertebrate groups that persist today, the extinction event at the Cretaceous-Tertiary (K/T) boundary, and the restructuring of the vertebrate megafauna dominated by mammals in the Paleocene and Eocene. Cretaceous turnover in the dinosaur fauna has been tied to the radiation and diversification of angiosperms, but these correlations do not apply to all continental regions represented by a fossil record. The Cretaceous also marks the emergence and radiation of certain groups of mammals, birds, lizards, and freshwater fishes. Reconstructions, however, that push back the diversification of modern lineages of birds and mammals (groups that include extant representatives) to the Early or middle Cretaceous are not supported by the fossil record. Despite the severity of the Cretaceous-Tertiary (K/T) extinction event of 65 million years ago, effects on vertebrates are strikingly selective, with a number of groups, including actinopterygians (ray-finned fishes), multituberculate mammals, eutherian mammals, turtles, lizards, champsosaurs, and crocodiles surviving across the K/T boundary. Subsequent to the K/T event, the basic organization and dynamics of the larger vertebrate fauna were radically transformed. Of general evolutionary interest is the protracted “rebound” of the larger vertebrate fauna and the nature of its controlling factors. The loss of the non-avian dinosaurs meant a loss of larger herbivorous browsers not replenished for some millions of years into the Paleocene. Diversification in the smaller mammal fauna shows a new emphasis on frugivory and granivory. Some of the modern groups of mammals first appear in the late Paleocene-early Eocene. Subsequent climate and habitat changes coincide with the radiation of large herbivorous mammals such as perissodactyls and artiodactyls. The coevolutionary relationships of the terrestrial mammalian megafauna and the changing flora likely promoted the spread of more open habitats that characterized the later Cenozoic.

The fossil record, like a daily clock, can be divided into any number of critical phases whose relative importance might reflect mere arbitration as much as objective evidence. Yet terrestrial ecosystems, including the vertebrates comprising them, experienced a particularly profound transformation between the beginning of the Cretaceous some 146 million years ago and the end of the Eocene epoch of the Tertiary between 40 and 34 million years ago. Why is this interval so remarkable? First, it begins with what has been called one of the most significant evolutionary events of life on land (Wing & Sues, 1992)—namely, the appearance and radiation in the middle Cretaceous of angiosperms and more modern insect groups, including key groups of pollinating insects. These dramatic radiations further set in motion important coevolutionary interactions between herbivorous vertebrates and diversifying angiosperm-dominated habitats (Weishampel & Norman, 1989) and established the framework for

modern ecosystems. Second, this interval encompasses the K/T extinction event, which had an unmistakable and profound ecological impact. The event is tied to the disappearance of several groups of terrestrial vertebrates (primarily non-avian dinosaurs) and the subsequent persistence and emergence of terrestrial mammals of radically smaller body size than dinosaurs and concomitantly different trophic connections with the flora. Third, this interval sets the stage for the rise of the modern mammal-dominated communities synchronous with the emergence of ecosystems involving fauna and flora that persist today.

The drama of these transitions notwithstanding, the Cretaceous-early Tertiary is marked by endurance as well as vicissitude. Indeed, one of the remarkable aspects of this phase is the resilience of many higher taxa—flowering plants, pollinating insects, even various vertebrate groups such as croc-

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odiles, lizards, turtles, frogs and salamanders, and certain mammals—that thwarted whatever shocks to the global system that came with the K/T extinction event. In its broadest outlines, “modern” terrestrial ecosystems essentially took form in the Cretaceous. Some organismic groups came and went, but the basic architecture of the present system is the legacy of the Late Mesozoic. This is not meant to minimize the waves of turnover that characterized many of the intervals thereafter. It is merely meant to emphasize that the new world established in the Cretaceous has, despite the K/T extinction event, more in common biologically with the living world than the Jurassic world. This paper is meant as an elaboration of this thesis drawing on a summary of the vertebrate record against what is known of relevant physical, environmental, faunal, and floral changes. The paper also addresses an important issue relating to the study of any geologic interval. This concerns the juxtaposition of theories of ecosystem change against what is actually known about the fossil evidence. Although such evidence includes anatomical and morphometric data for inferring ecological roles in fossil taxa, the major and most critical aspect of the evidence concerns distributions of taxa in space and time. Such distributions are based on raw occurrence data and ranges inferred (but not necessarily observed) from reconstructed phylogenies (Norell, 1992; Norell & Novacek, 1992).

THE CRETACEOUS-EARLY TERTIARY RECORD

GEOGRAPHIC PATTERNS

Advances in paleogeographic reconstruction have been fed by data from sea floor spreading patterns, polar wander curves, and many other sources. The intensity of that coverage has not spared the Cretaceous-early Tertiary. Here are just a few salient aspects of the broad-scale geographic history of this interval, covered to much greater depth in the references cited.

By the Cretaceous, the fragmentation and drifting of continental blocks well under way in the Jurassic (Fig. 1) had transformed the terrestrial geography of the globe (see Smith et al., 1994; Scotese, 1997). This fragmentation on a gigantic scale, the so-called break up of Pangea, represents a reversal in the pattern of continental coalescence recorded in the earlier Mesozoic. Its potential influence in isolating and reshaping the biota is obvious. A vast belt of amphitropical seaway, the Tethys, split Pangea asunder, isolating the Gondwana landmasses from the northern Laurasian blocks. Both these Pangean subdivisions were subjected to further

fragmentation (Fig. 2). While Africa and South America still remained sutured across the Amazon-Gabon basin region in the Early Cretaceous, this connection was being severed by the opening of the Atlantic both in the north and south. Other southern blocks, such as Antarctica and India, became separated from the Gondwana core. Western and southern Europe were a fragmented mosaic of landmasses: an archipelago in the nascent northern Atlantic and a huge embayment in the region of present-day eastern Europe and Russia. North America, isolated from both South America and northern Africa by formidable oceanic barriers, was also flooded by epicontinental seas, especially along its western margin. The massive supercontinent of Asia was also eroded along its southern and western margins by extensive seaways. The long arm of its Siberian extension made only intermittent and tenuous connections with the Alaska region of North America.

This trend toward continental fission and marine ingression reached its acme in the Latest Cretaceous (Smith et al., 1994; Scotese, 1997). South America and Africa were well separated by the southern Atlantic (Fig. 3). Europe was still very much an archipelago. North America was essentially two landmasses nearly bisected by a north-south epicontinental seaway in what is now the Western Plains-Rocky Mountain area. A similar seaway separated fragments of western from eastern Asia. There is both geologic and paleontologic evidence for a corridor between Siberia and Alaska, but this connection was, as in earlier times, ephemeral, depending on the cycles of marine ingression that characterized this phase. Indeed, so profound is the fragmentation of large landmasses in the middle and Late Cretaceous that it has been associated with the isolation and diversification of modern and extant lineages of birds and mammals, at a time before that diversification is indicated by the first occurrences of representative fossils (see Hedges et al., 1996; Kumar & Hedges, 1998; and discussion below).

The Paleocene terrestrial world is the expected product of the continental fission in the Late Mesozoic. Southern landmasses like Antarctica, India, and Madagascar were further isolated from their original moorings. Yet in the early to middle Paleocene there is evidence of reversal in the pattern of marine invasion that so characterized the later Cretaceous. The mid-epicontinental seaway in North America had retreated to an embayment along the continent's southern margin, a mere extension of what is the present-day Gulf of Mexico. Europe and western Asia, though still separated from eastern

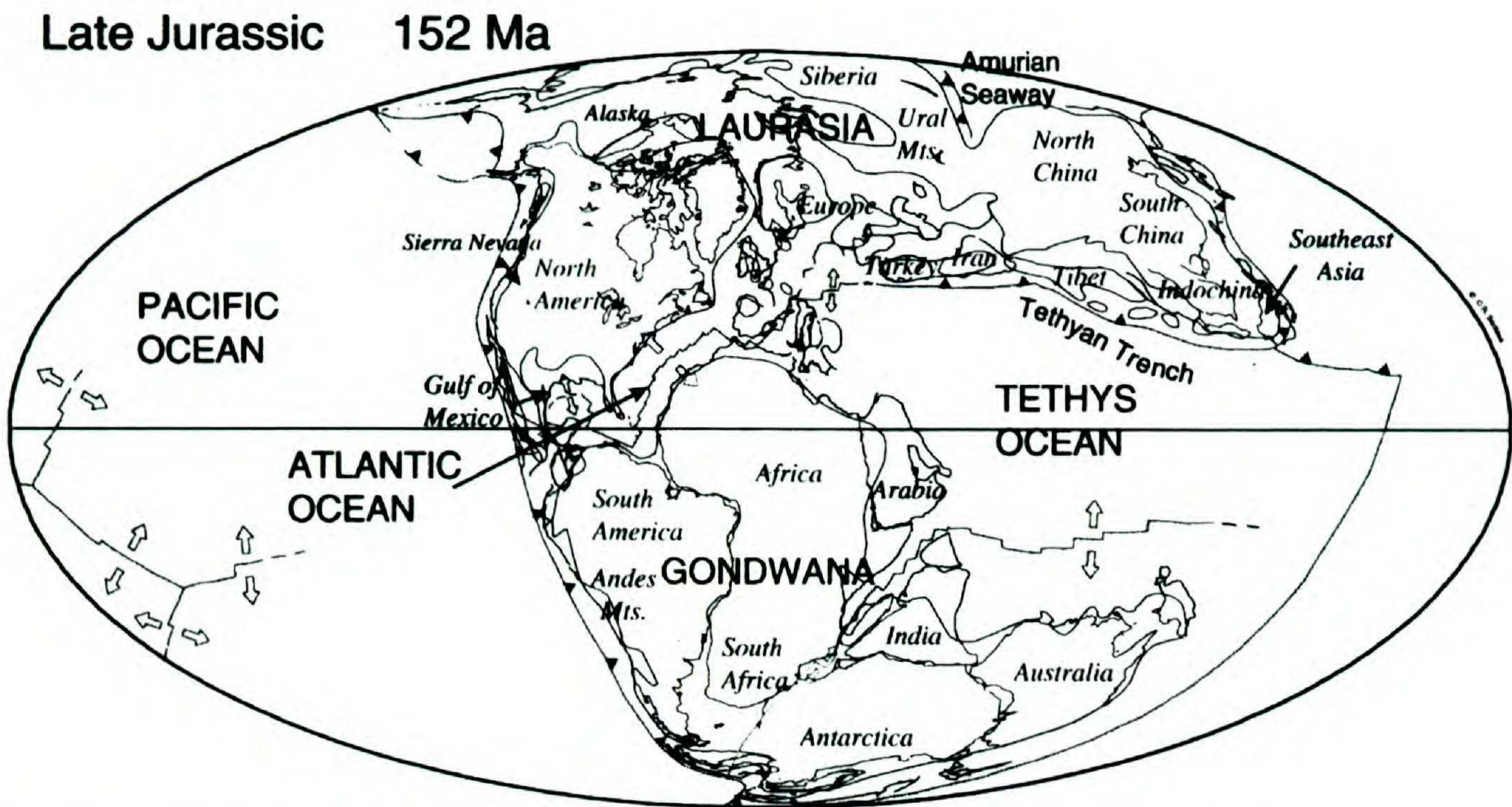


Figure 1. Reconstruction of continental positions for the Late Jurassic. Map from Scotese (1997).

Asia by the north-south trending Turgai straits (Szalay & McKenna, 1971), showed more coalescence than during the previous interval. Importantly, stronger and more enduring connections were forged between Europe and eastern North America as well as between Asia and North America in the Bering region. Opportunities for biotic exchange across emergent landmasses are also evident from the common occurrence of various mammal taxa across the northern continents (Szalay & McKenna,

1971; Savage & Russell, 1983; Janis, 1993; Beard, 1998).

These northern land connections were maintained in the early Eocene (ca. 55 million mybp), but a notable break between eastern North America and Europe did occur with the merging of the far northern Atlantic with the Arctic oceans by middle Eocene times (Fig. 4). This isolation event was mirrored by the subsequent divergence of European and North American mammal faunas (McKenna,

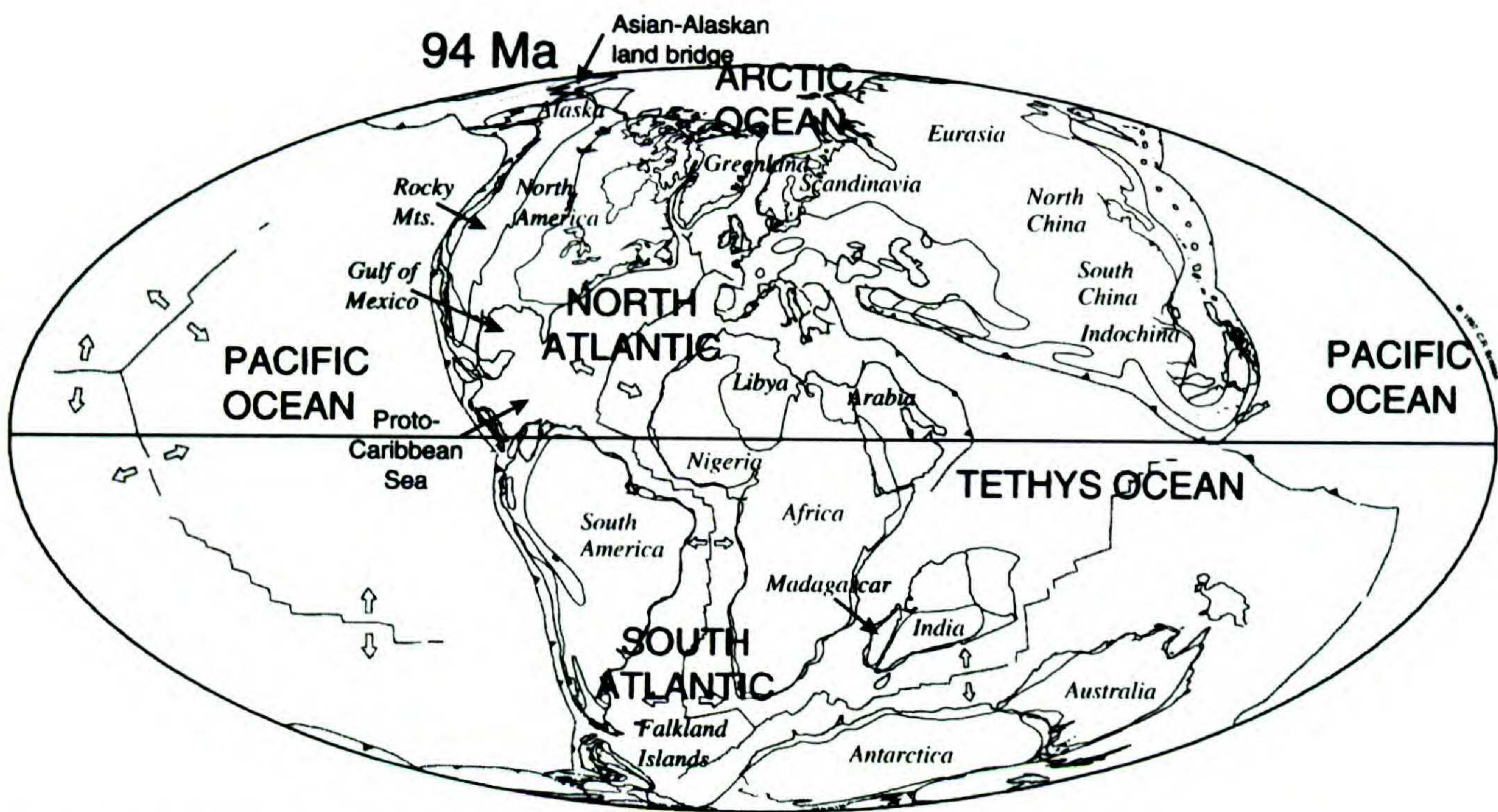


Figure 2. Reconstruction of continental positions for the Mid Cretaceous. Map from Scotese (1997).

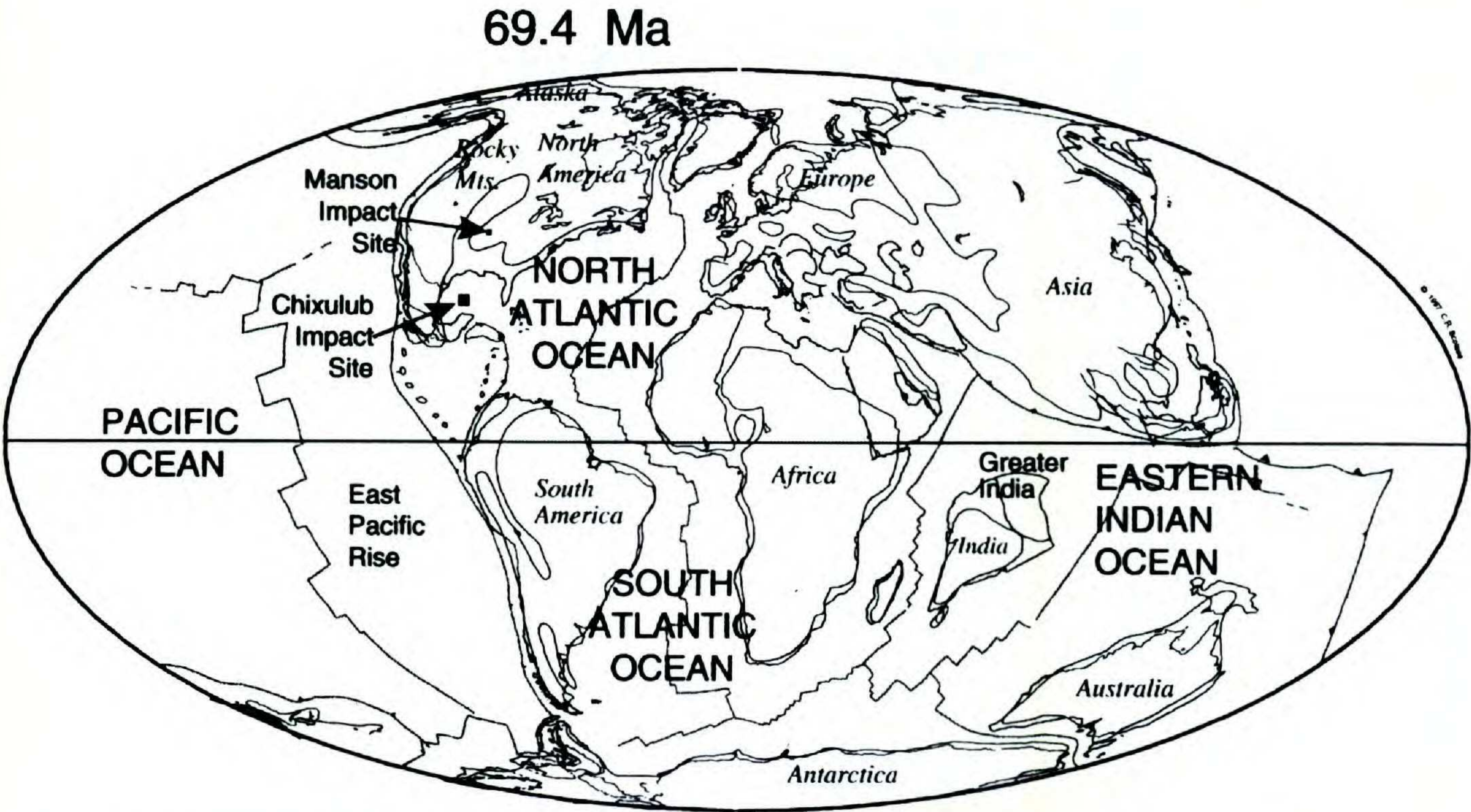


Figure 3. Reconstruction of continental positions for the Late Cretaceous. Map from Scotese (1997).

1983; Flynn, 1986). During the Eocene, the far southern landmasses showed increasing isolation, with India drifting farther northward toward the underbelly of Asia and the Antarctica-Australia megamass drifting from southern South America and Africa. Although some dispersal to South America from either Africa or North America is suggested by the Eocene mammalian record, any such migrations were over substantial tracts of ocean. Indeed, South America remained essentially a giant island

through most of the Cenozoic, preceding the closure of the Panamanian land bridge and a marked exchange in fauna between the Americas in the Pliocene between 2.7 and 2.5 million mybp (Marshall & Cifelli, 1990; Woodburne & Swisher, 1995). Not all trends in the middle and later Eocene, however, involved a reprise of continental isolation and separation. Further regression of the mid-latitudinal Tethys seaway in the region of the present-day Mediterranean Sea (Scotese, 1997) enhanced pos-

Middle Eocene 50.2 Ma

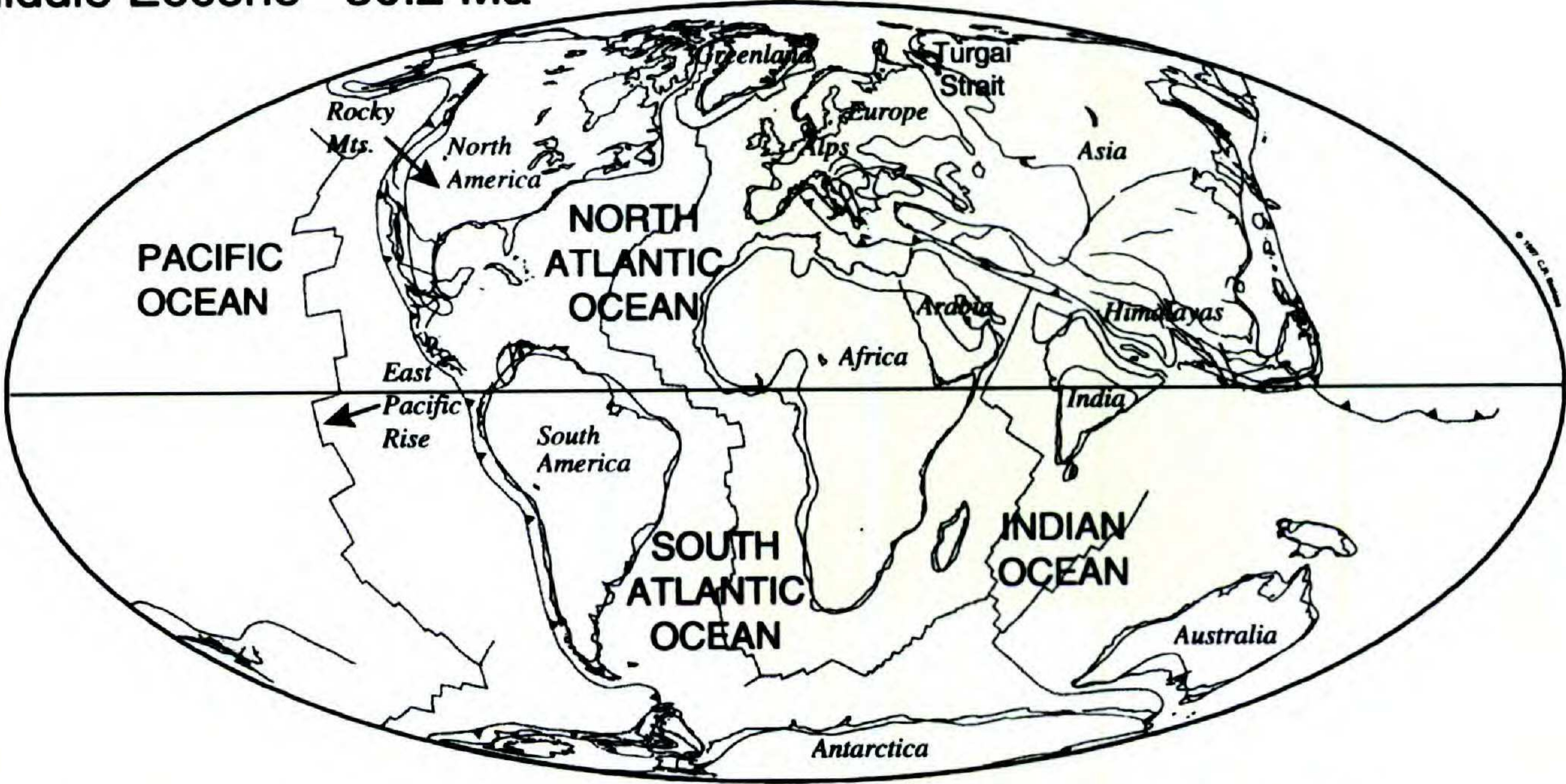


Figure 4. Reconstruction of continental positions for the Middle Eocene. Map from Scotese (1997).

sibilities for biotic exchange between Africa and Europe and western Asia.

To summarize, the oscillation of continental fragmentation and coalescence during the Cretaceous-Early Tertiary is particularly dynamic and is better chronicled than geographic change during earlier intervals. Highlights of this phase include the marked isolation of many landmasses during the Cretaceous, a pattern related to geographic differences noted among terrestrial floras and faunas (Wing & Sues, 1992). By the Late Cretaceous, the amount of marine ingression, in combination with continental fragmentation, produced a marked extent of shallow epicontinental seas, continental shelves, and coastline. Many of the best-known vertebrate assemblages, such as the Late Cretaceous localities in the western interior of North America, represent communities at the margin of these seas. As noted above, it is appealing to relate the diversification of some major clades of more modern vertebrates, e.g., birds and mammals, to the pulse of continental rifting and fragmentation that occurred in the Middle to Late Cretaceous (Hedges et al., 1996). Yet the fossil record does not so far show evidence of extensive radiation of such groups at such an early time (see discussion below). Nonetheless, a degree of endemism for certain vertebrate groups can be documented. For example, a diverse group of Mesozoic and early Tertiary herbivorous mammals, the multituberculates, are well represented in Late Cretaceous assemblages from both North America and central Asia. Virtually all the multituberculate taxa represented in either continent are, however, highly distinctive. Most of the central Asian taxa from rich Mongolian sites have even been identified as an endemic, monophyletic group (Rougier et al., 1997). This obtains despite the fact that central Asia and western North America were at least intermittently connected through Siberia-Alaska in the Late Cretaceous.

In the early Tertiary, patterns of continental isolation, and their biotic effects, differ between the northern and Southern Hemispheres. In the north, landmasses were relatively stabilized and interchange, or isolation, of the vertebrate fauna tracked the severance or suture of land connections between western and eastern Asia, eastern Asia and North America, and Europe and North America. Expectedly, a marked similarity among Holarctic vertebrate faunas has long been recognized. Moreover, Asia has been increasingly recognized as a staging area for the invasion of many higher-level mammalian taxa (e.g., primates, rodents, lagomorphs, perissodactyls, artiodactyls, cetaceans, and others) into North America (Beard, 1998). Homog-

enization of mammalian faunas between North America and Europe is especially apparent during certain intervals like the early Eocene where northern connections were broadly developed (Savage & Russell, 1983). In the south, by contrast, the break-up of Gondwana initiated in the middle Mesozoic progressed, with further rifting and drift of India, Antarctica, Australia, and other landmasses. Doubtless, this geologic fragmentation contributed substantially to the marked patterns of endemism in present-day fauna and flora documented for the southern continents. Unfortunately, the early Tertiary vertebrate record is less complete and less geographically comprehensive in the Southern Hemisphere. Although important fossil localities document a rich and highly endemic mammalian fauna in South America, early Tertiary faunas in continents such as Australia are limited. A small sample of Eocene mammals from Antarctica (polydolopoid marsupials, edentates, and ungulates) indicates faunal relationships between that continent and South America (Woodburne & Zinsmeister, 1982; Hooker, 1992). The early Tertiary vertebrate record for Africa is extremely poor, a hiatus that critically constrains reconstructions of the diversification and deployment of vertebrates from the southern continents.

CLIMATIC PATTERNS

Continental drift, sea level rise and fall, and oceanic circulation during the Cretaceous-early Tertiary "age of fragmentation" obviously relate to global climatic patterns whose documentation is rapidly improving. Much of the evidence here comes from fossil pollen and plant localities (see below) as well as isotopic analysis for paleotemperatures. Naturally, the late Mesozoic-early Cenozoic global climate, as today, was a mosaic of climatic regimes, some of which are much more precisely documented than are others. Yet some generalizations about overall trends are possible, as temperature curves, especially in the case of the northern latitudes, have distinctive profiles (see Fig. 5 and Burchardt, 1978; Wolfe, 1978; Janis, 1993; Askin & Spicer, 1995).

The earliest phase of the Cretaceous generally experienced a warming trend that peaked about 100 million years ago. Thereafter a slow and steady decline in mean temperature ended in a rather abrupt drop in the last few million years of the Cretaceous. Fossil wood and oxygen isotope data derived from marine mollusk shells of the Antarctic Peninsula also record declining temperatures during the Santonian-Campanian interval to the Maastrichtian during the Late Cretaceous (Pirrie & Mar-

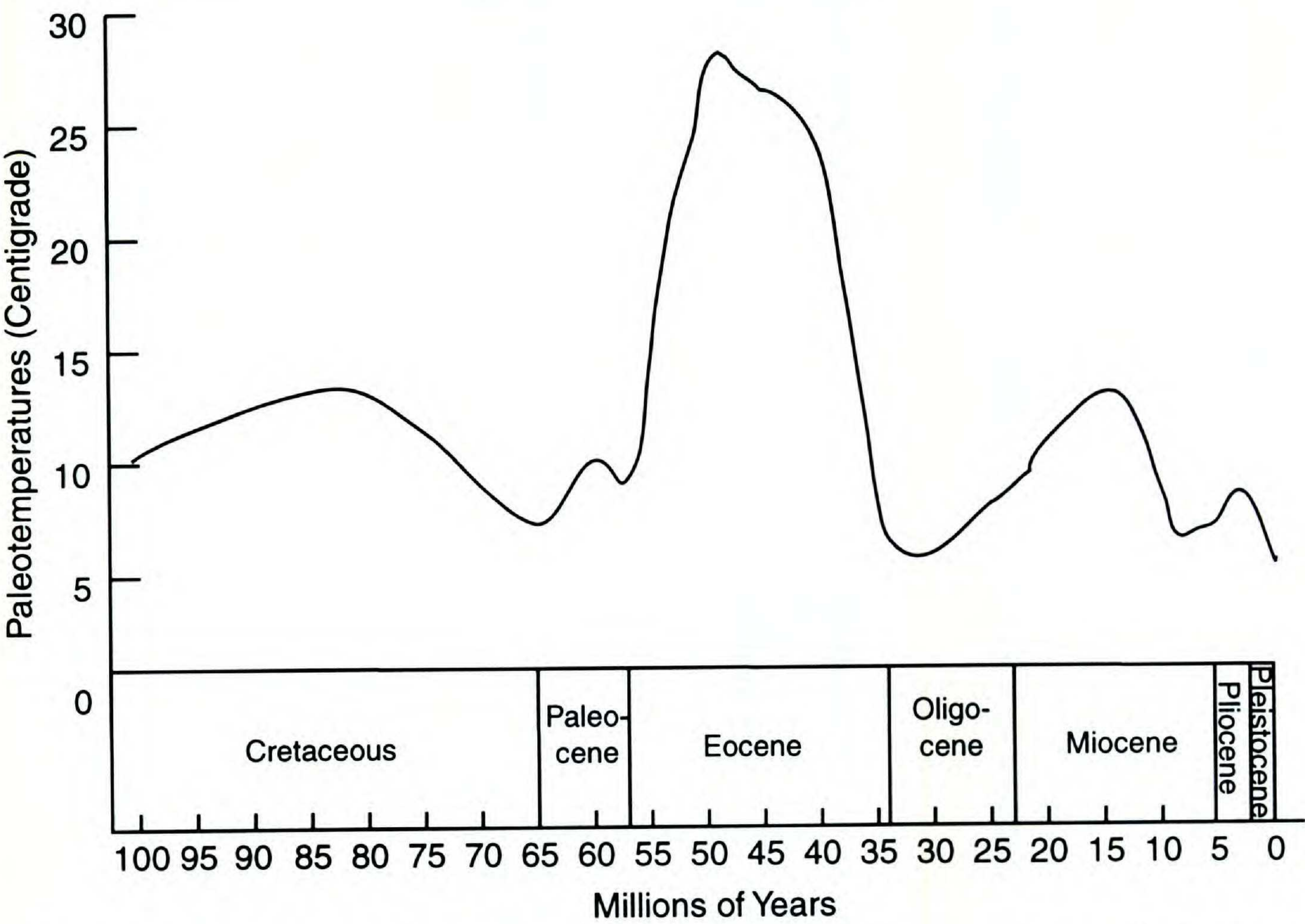


Figure 5. Curve for mean annual temperature in northern latitudes derived from oxygen isotope and paleobotanical data. After information in Burchardt (1978), Wolfe (1978), Janis (1993), and Askin & Spicer (1995).

shall, 1990). Similar patterns are indicated in both northern and southern latitudes: Late Cretaceous cooling was global.

The early Cenozoic in general shows a reversal in this global cooling pattern. A warm early Paleocene was succeeded by an even more tropical middle Paleocene (see Janis, 1993, and references cited therein). Temperatures retreated in the late Paleocene, but the lapse was temporary. The early Eocene was a time of dramatic rise in global temperature and marked equability. Indeed, tropical habitats are evident at very high latitudes, and the cosmopolitan nature of fauna and flora, especially in the holarctic continents, is striking. By the end of the early Eocene (about 51 Ma), this warming trend reached a thermal global high for the entire Tertiary (Fig. 5). A cooling and drying phase beginning in the middle Eocene accelerated markedly between 43 and 40 Ma and continued through the end of the Eocene. The more marked seasonality and climatic latitudinal zonation that came with this cooling trend likely influenced the coincident turnover in mammal lineages, and the radiation of larger more modern mammal groups that persisted through the rest of the Cenozoic (Prothero, 1985;

Janis, 1993). Such turnover was also likely promoted by mammalian dispersal and immigration, especially in Holarctica where continents were broadly, if intermittently, connected. Although the affect of climate on such dispersal seems to have been indirect for much of the Cenozoic, the relationship between climate, sea level change, and mammalian faunal exchange is strongly etched for the late Eocene-early Oligocene transition (Woodburne & Swisher, 1995). Indeed, the interplay of climatic and biotic change relates to the controversy over the boundary line for the end of the Eocene (Prothero & Berggren, 1992). A major climatic shift occurred about 40 million years ago, but a major biotic reshuffling, well documented in the case of mammals, occurred over an extended transition span of about 16 million years between the middle Eocene and through most of the Oligocene.

Again, it is important to note that these general global scale trends in temperature should not obscure the heterogeneity in climatic regimes that also characterized different, shorter-term phases of the late Mesozoic and early Cenozoic. In the Early to middle Cretaceous, climates at midlatitudes (southern Laurasia and northern Gondwana) were

seasonally dry, but the dominance of fern and conifer palynomorphs in northern Laurasian and southern Gondwanan regions indicated cooler and wetter climates (Brenner, 1976; Ziegler et al., 1987). Late Cretaceous climatic regimes were doubtless diverse, as indicated by the pastiche of different floras in higher and lower latitudes (see review in Wing & Sues, 1992). Higher-latitude floras show greater loss of diversity with the climatic deterioration in the last (Maastrichtian) age of the Cretaceous. But the heterogeneity in climate is not simply indicated by variance in the composition of paleofloras. During the Late Cretaceous, major areas, such as Central Asia, preserve extensive sand dunes, abundant dinosaurs, mammals, and other vertebrates, but few plant remains. These were environments subject to intense drying and seasonality, mixed with intermittent torrential rains and flash floods. Such conditions are typical of deserts or semi-arid regions today (Jerzykiewicz et al., 1993; Loope et al., 1998).

A mosaic of climatic regimes is also apparent in the early Tertiary. There is evidence of a sharp but long-lasting transition to wetter climates over most of North America in the early Paleocene (Fastovsky & McSweeney, 1987; Retallack et al., 1987; Wolfe & Upchurch, 1987; Lehman, 1990), a shift that has been related by some authors (Wolfe & Upchurch, 1987) to the effects of the K/T bolide impact. Nonetheless, higher latitudes of both North America and Asia probably maintained extensive subtropical woodland or gallery forests typical of drier, more seasonal climates. The marked warming trend in the early Eocene clearly expanded the tropical rainforests through higher latitudes, but a narrow belt of more seasonal climates probably remained in the far north of Asia and North Africa, as well as in parts of Antarctica and Australia (Janis, 1993). Expectedly, the contraction of tropical rainforest habitat, and the expansion of habitats that indicate drier and more seasonal climates—namely, paratropical forests, more open woodlands, and temperate forests (mixed coniferous and deciduous)—accompanied the marked global cooling trend in the later Eocene (Miller, 1992). Likewise, the Eocene/Oligocene boundary in the marine realm shows a sharp increase in temperature seasonality similar to that indicated by contemporaneous terrestrial floras (Swisher & Prothero, 1990).

EXTRATERRESTRIAL IMPACTS AND VOLCANISM

In addition to changing geography, sea level, and climate, other physical environmental events doubtless have wide-ranging and enduring effects

on the biota. Notable among those events cited for the late Mesozoic and early Cenozoic are extraterrestrial impacts and pulses of volcanism. Archibald (1996a) provided a very useful overview of these occurrences in the geologic record and their likely affects. The timing and reality of a major bolide impact at the end of the Cretaceous (ca. 65 million years ago) is now widely recognized (Alvarez et al., 1982). The evidence for impact is the preservation of the massive (110 miles in diameter) Chicxulub Crater near the Yucatan Peninsula of Mexico. Attendant disasters have been widely imagined and reconstructed; they include but are not restricted to global cooling due to prolonged cloud cover (Alvarez & Asaro, 1990), acid rain (D'Hondt et al., 1994), and global wildfire (Wolbach et al., 1990). Although such catastrophic phenomena are certainly expected, matching these events with a highly selective pattern of extinction, especially in the terrestrial record, is problematic (see further discussion below). There is geologic evidence for other much smaller bolide impacts in the Early Cretaceous, the Late Cretaceous just preceding the Chicxulub impact, and in the early Tertiary (Grieve & Robertson, 1987; Newsom et al., 1990; Raup, 1991; Izett et al., 1993; Hildebrand et al., 1995). The timing and relation of these smaller impacts to major pulses of extinction and turnover are not clearly documented.

A second physical trauma related to extinction patterns is widespread volcanism. Even isolated volcanic eruptions, like the recent Mount Pinatubo eruption in the Philippines, can dramatically influence present-day weather patterns. One can imagine the magnitude of such effects with volcanism on a much wider scale. Marked phases of volcanism are recorded throughout the Cretaceous-early Tertiary interval, but the greatest intensity of broad-scale volcanism seems coincident with the K/T boundary (Courillot, 1990; Campbell et al., 1992). Flood basalt data taken from the Deccan Traps of India suggest an enormous volume of lava: as much as 350,000 cubic miles. It has been argued that the Deccan event would have produced significant atmospheric changes, such as increased ash and other particulate matter, carbon dioxide, and cloud cover, that may have induced either global warming (through the greenhouse effect) or global cooling (an option more in line with the recorded drop in global temperature at the end of the Cretaceous). Another scenario ties volcanic eruption and the release into the atmosphere of elements like selenium that could be harmful to the developing embryos of dinosaurs and other vertebrates. Selenium or other possibly toxic trace elements have been identified

in the eggshells of dinosaurs from localities at or near the K/T boundary (Hansen, 1991; Stets et al., 1995), although there is little comparative data on eggs from older Cretaceous levels. As in the case of the bolide impact, the most straightforward effect of marked volcanism would be cloud cover, atmospheric accumulation of carbon dioxide, prolonged darkness, climatic cooling, and possible temporary disruption of photosynthesis (Archibald, 1996a).

The hypothesized link between marked volcanism and the K/T extinction event, however, does entail problems. The Deccan event may have been much broader in time than the extinction event—between 69 and 65 million years ago (Prasad et al., 1994). This broad span, as well as the nature of the Deccan basalts, suggests continual and long-term activity much like the shield volcanoes of Hawaii rather than sudden and catastrophic explosions like the eruption of Mount Saint Helens. Moreover, intense volcanic activity, like the bolide impact, does not effectively explain the highly selective extinction at the K/T boundary (see below).

THE TERRESTRIAL FLORAL RECORD

Major contributions to this issue of the *Annals* deal with the dramatic floral changes of the late Mesozoic-early Cenozoic. The summary here derives from those papers and a few earlier reviews, notably Wing and Sues (1992) and Askin and Spicer (1995).

Earliest Cretaceous floras were generally thought to lack angiosperms and to look like preceding Late Jurassic floras, but pollen data from strata of Hauterivian age and scattered records from the Valanginian, now show that angiosperms were well established by the earliest Cretaceous (Friis et al., 1999). The record is nonetheless spotty, with diverse floras found mainly in terrestrial strata with poor age control, or more readily datable marine strata with depauperate floras. By Barremian-Aptian times rapid diversification of angiosperms is evident, though this radiation seems less explosive at middle to high latitudes where extensive ferns suggest persistence of open foliage (Wing & Sues, 1992).

Early Late Cretaceous angiosperm diversity increased dramatically, especially in middle and high latitudes. By the end of the Late Cretaceous, 50–80% of the fossil flora were flowering plants (Crabtree, 1987; Lidgard & Crane, 1990). This radiation was coincident with a significant drop in diversity and abundance of cycadophytes and ferns, but not a decline in the proportion of conifer species in these assemblages (Lidgard & Crane, 1990). In-

deed, specimen counts at the Late Cretaceous Black Hawk locality show that 4 of the 9 taxa represented by more than 100 specimens (out of a total of 7400 specimens) are conifers or cycadophytes (Parker, 1976). The data suggest a Late Cretaceous co-dominance of gymnosperms with flowering plants, at least in certain localities where such a census is feasible.

This diversification notwithstanding, angiosperms, prior to the Campanian and Maastrichtian, did not compare with the present-day angiosperm floras in their range of ecological roles. Angiosperm wood is rarer than contemporaneous flowers, as well as coniferous wood (Wing & Tiffney, 1987). In addition, latitudinal variation in angiosperm diversity persisted throughout the Cretaceous. For example, Cretaceous floras from Alaska show a lower proportion of angiosperms than do lower-latitude floras (Spicer & Parrish, 1986; Parrish & Spicer, 1988). By Maastrichtian times, these high-latitude floras were drastically reduced in diversity and show signs of lower productivity (Spicer & Parrish, 1986), plausibly a result of Late Cretaceous climatic deterioration. A more stable pattern of diversity and productivity, however, is indicated in Antarctica during the Late Cretaceous (Askin & Spicer, 1995).

Following the K/T event, the replenishment and diversification of angiosperms shows marked heterogeneity on a global scale. This has strong implications for any scenario concerning the range and magnitude of the extinction event, its cause, and its effects on the biota. In the North American earliest Paleocene a drastic decrease in angiosperms is indicated by the presence of a “fern spike” only a few centimeters above the K/T boundary (Orth et al., 1981; Nichols et al., 1986). This fern flora was succeeded by an angiosperm-dominated flora of quite different composition than the conifer-abundant floras of the latest Cretaceous of North America (Orth et al., 1981; Tschudy et al., 1984; Tschudy & Tschudy, 1986). Wolfe (1987) attributed preferential extinction of evergreen species at the K/T boundary to relatively low tolerance to the cold snap caused by the impact cloud. But the floral record for North America displays notable variation. Megaflores in New Mexico and Colorado show low diversity for the first few million years of the Paleocene (Wolfe & Upchurch, 1986, 1987), but floras in western North Dakota show a more rapid increase in diversity (Johnson et al., 1989; Johnson & Hickey, 1991).

One of the most provocative aspects of the paleobotanical evidence is that the dramatic fall-off in angiosperm, indeed floral, diversity at the K/T

boundary does not hold for certain other regions of the world. Paleofloras from Japan (Saito et al., 1986), New Zealand (Raine, 1988), and Seymour Island off Antarctica (Askin, 1988) show little or no turnover at the boundary. This is in strong contrast to the terrestrial faunal picture, where non-avian dinosaurs were supposedly decimated worldwide (but see discussion below on the paucity of non-North American vertebrate sites bracketing the K/T boundary) and the large tetrapod herbivore component was erased. The discrepancy in the global pattern between faunal and floral change still eludes explanation.

Early-middle Paleocene floras of the Northern Hemisphere show low diversity and strong homogeneity, as exemplified by very similar floras from the late Paleocene of Mongolia, China, and western North America (Crane et al., 1990; Manchester, 1999). During the early Eocene the rise in global paleotemperatures corresponds with a high point in tropicality and the flourishing of angiosperm-dominated closed forests; subtropical vegetation may have ranged as far north as 60° latitude and multistratal tropical rainforests occurred at 30°N (Wolfe, 1985). In the Eocene, Australia (then between 30 and 60°S) harbored diverse angiosperm-dominated tropical to subtropical rainforests (Hill, 1982). Argentine floras were tropical but were subject to seasonal wet and dry periods (Romero, 1986). The African floral record shows evidence of wet tropical forests beginning in the middle Tertiary, though such habitats likely did not spread on a continental scale until the Miocene (Axelrod & Raven, 1978). Late Eocene floras from Egypt were wet and tropical with indications of seasonality (Wing & Sues, 1992).

The cooling and drying phase during the middle to late Eocene doubtless inaugurated the extinction or marginalization of the thermophilic plants (Manchester, 1999). Likewise, increased aridity during the late Eocene in the Rocky Mountain region promoted loss of conifers, even in wetter habitats at lower elevations (Wing, 1987). A global decline in temperatures and greater seasonality at about 33 Ma resulted in a shift to more broad-leaved types of vegetation in coastal North America (Wolfe, 1978), a pattern essentially duplicated in Europe (Collinson & Hooker, 1987). It is noteworthy that by mid-Oligocene, most woody genera that typify modern North American forests were already present (Manchester, 1999). Thus floral changes, as well as vertebrate faunal turnover, during the late Eocene-early Oligocene interval established the persisting terrestrial ecosystems of most continents.

The plant record, therefore, shows both oscilla-

tion and resilience during the late Mesozoic-early Tertiary. Angiosperm floras, though still spottily sampled, were definitely established by the earliest Cretaceous (Crane & Lidgard, 1990). Angiosperm diversification, though subject to a number of pulses, seems to have been progressive rather than instantaneous during the Cretaceous. Differences in these patterns of diversification from the Late Cretaceous through the early Cenozoic in high-latitude northern and southern regions can be attributed to different continental configurations. The extensive continuity of land in the north favored floral dispersal in contrast to Antarctica and adjacent landmasses, which offered increasingly restricted dispersal corridors (Askin & Spicer, 1995). Considerable floral heterogeneity, including the persistence of more open vegetation during the Cretaceous at certain latitudes and on certain continents, also has been related to the trophic impact of large terrestrial herbivores, namely dinosaurs (see below). Heterogeneity likewise obtains for the global pattern of floral extinction and replacement at the K/T boundary. In North America, turnover of the flora is marked, but in Asia and the Southern Hemisphere little turnover coincident with the K/T event is evident. In the Paleocene and early Eocene, floral diversification was fed by global warming and the concomitant latitudinal spread of tropical and subtropical forests. Homogeneity among Northern Hemisphere early Eocene floras matches that seen in the vertebrate fauna. Starting in the middle Eocene, marked global cooling and increasing aridity catalyzed the loss or restriction of these warm temperature floras and their replacement, by the early-middle Oligocene, by woody-dominated floras that essentially persist today.

THE TERRESTRIAL FAUNAL RECORD: NON-VERTEBRATES

The terrestrial non-vertebrate fauna obviously encompasses a vast range of organisms, including freshwater invertebrates, soil infauna, protozoans, and microbes. Yet the biostratigraphic record for these elements is generally so poor that it provides little insight on biotic transitions of non-vertebrates during the late Mesozoic-early Cenozoic. Brief discussion here is restricted to insects where the record, though inconsistent, is impressive and rapidly improving. Comprehensive treatment of the early fossil record of pollinating insects can be found in D. Grimaldi's contribution to this volume (Grimaldi, 1999). The first occurrences of aphids (Homoptera), short-horned grasshoppers (Orthoptera), and gall wasps (Hymenoptera) are in the Cretaceous. The equivocal Late Cretaceous record of ants (Hennig,

1981; Wilson, 1987; Agosti et al., 1998) is now confidently established based on well-preserved specimens in Turonian-age (Late Cretaceous) amber from New Jersey in the northeastern United States (Agosti et al., 1998).

Perhaps the most interesting aspect of the insect record in the Cretaceous is the radiation of pollinating insects. The major groups in question are the Lepidoptera (butterflies and moths), Hymenoptera (bees, wasps), and Diptera (flies) within the Brachycera. Lepidoptera have a clear record since the Early Cretaceous (Whalley, 1986), but there is evidence of their first appearance in the Upper Jurassic with extensive diversification in the middle to Late Cretaceous (Grimaldi, 1999). Likewise, the Brachycera have a record dating back to the Upper Jurassic. The pollination motive in Late Cretaceous angiosperms seems somewhat different than that in mid-Tertiary floras. Most flowers were radially symmetrical (actinomorphic) and probably either pollinated by wind or by a broad range of insects rather than just the Hymenoptera (Friis & Crepet, 1987; Crepet & Friis, 1987). But advanced eusocial bees are known from the Campanian (Michener & Grimaldi, 1988), and the presence of lauraceous flowers in the Cenomanian is consistent with bee pollination (Drinnan et al., 1990). A suggested lag between the rise of angiosperms and a putative later appearance of pollinating insects has been disputed (Grimaldi, 1999). Assessment of fossil occurrence data against patterns of phylogeny suggests a coincidence between the radiation of angiosperms and their insect pollinators, a coincidence expected by the strong ecological interdependence of these groups.

The fossil record suggests a continual increase in the number of insect families throughout the Paleocene, with the appearance of modern groups of moths and butterflies by the Eocene. Formicoid ants also show significant diversification from the Late Cretaceous through the Paleocene (Wilson, 1987).

The insect record for this crucial interval is of course still patchy. Yet what we know of this record seems to indicate two essential patterns of insect evolution. First, the radiation of pollinating insects is now extended back to a time coincident with the radiation of flowering plants. Second, there is no evidence of perturbation of insect diversification that is clearly related to the K/T extinction event.

THE TERRESTRIAL FAUNAL RECORD: VERTEBRATES

Although vertebrates have a much more enriched record of faunal change from the Cretaceous

through the early Cenozoic than do other animal groups, the emphasis of that history largely concerns the non-avian dinosaurs and mammals. For the sake of completeness, the basic aspects of the known record of the major terrestrial and freshwater vertebrate groups (Fig. 6) are provided here, with the weight of the discussion centering on the groups with particularly well-documented records. These summaries focus on distribution evidence for groups during the Late Cretaceous-early Tertiary, with emphasis on differential survival across the K/T boundary.

Elasmobranchs. Sharks, rays, and relatives have a long and comparatively rich fossil record, to a large extent due to the abundance of taxonomically informative teeth. The tooth record is complemented in some cases by spectacular fossils of calcified cartilaginous skeletons. The elasmobranch fossil record, which is overwhelmingly marine, is notable for the waves of succession of major groups (Capetta et al., 1993). Many archaic clades traditionally known as families of the mid and late Paleozoic dwindled or went extinct by the Triassic. The Mesozoic radiation comprised clades extending back to the Carboniferous (e.g., Polyacrodontidae), clades originating in the Triassic or Jurassic but disappearing by the earliest Tertiary (e.g., Orthacodontidae), and clades first appearing in the Jurassic or Cretaceous and persisting through the Cenozoic to the present day (e.g., several squalimorph, squatinomorph, and galeomorph familial lines). The lineages emerging during the later Mesozoic far outnumber the modern higher clades that have first occurrences in the Tertiary (e.g., Heptranchidae, Dalatiinae, and Rhincodontidae).

The persistence of higher clades of elasmobranchs across the K/T boundary contrasts with some evidence for at least local extinction at the species level. Archibald and Bryant (1990) and Archibald (1996a) documented the disappearance in lowermost Paleocene beds of five species of elasmobranchs known from the uppermost Cretaceous Hell Creek beds of Montana. These species were freshwater forms, as the fossil localities in the Hell Creek Formation represent habitats that were 100 to 150 miles west of the receding epicontinental marine sea. Thus these freshwater sharks and rays seemed to have been among the victims of the K/T extinction event, at least where sufficient evidence exists in the North American record.

Bony fishes. The present-day diversity of bony fishes (Osteichthyes) is overwhelmingly embraced by the actinopterygian or ray-finned fishes, which number above 20,000 species, nearly half the

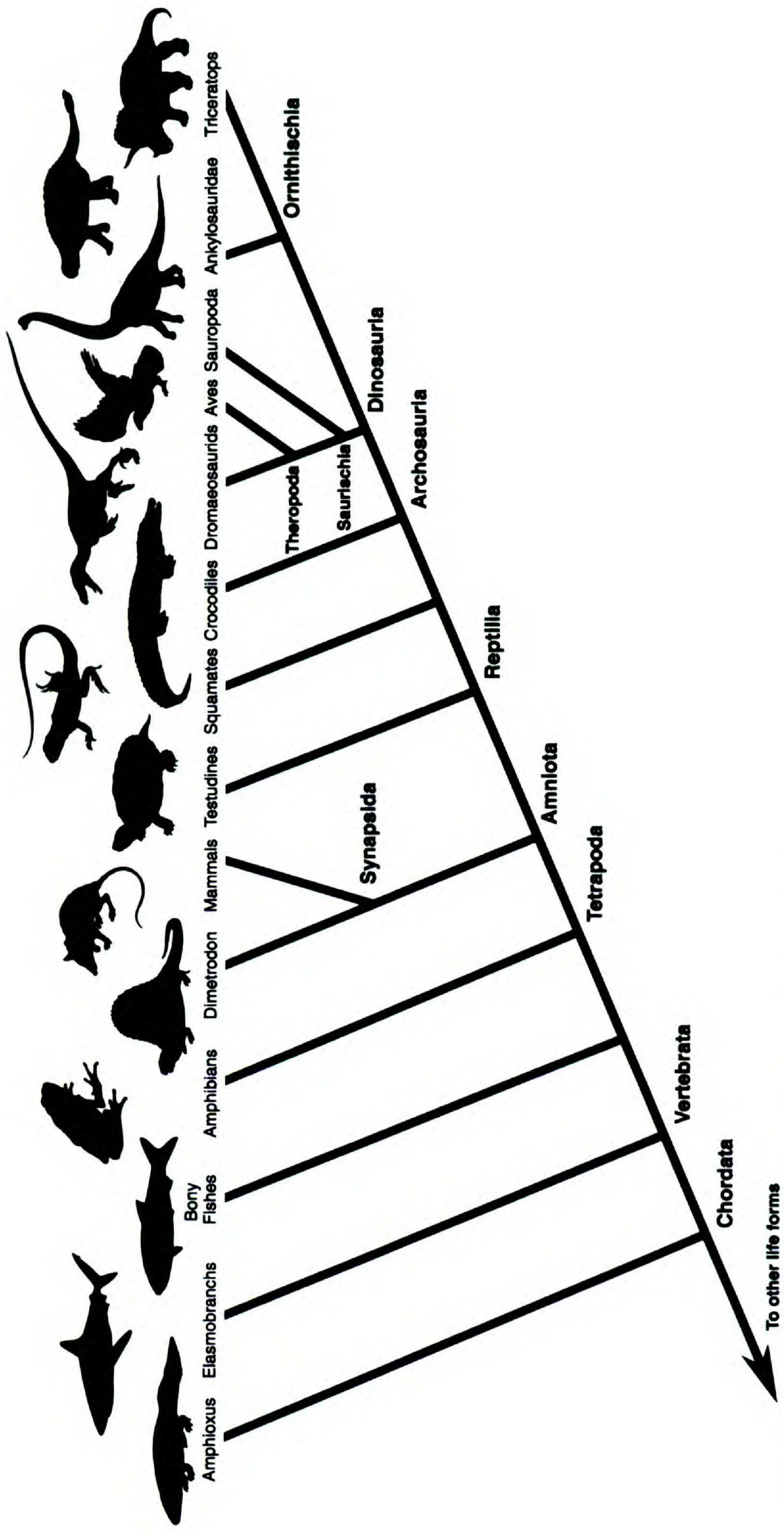


Figure 6. Cladogram depicting interrelationships of the major vertebrate clades.

named species of all living vertebrates (Moyle & Cech, 1988). This great radiation began at least by the Silurian, with the appearance and short duration of *Andreolepis*, followed by the Devonian and Carboniferous radiation of many archaic clades (Gardiner, 1993). Waves of successive clades of basal actinopterygians also characterize the Triassic and, to a lesser extent, the Jurassic and Cretaceous (Gardiner, 1993). The spectacular diversification of clades of more modern bony fishes, the teleosts, began at least in the Early Mesozoic, with an impressive number of lineages recorded by the Cretaceous (Patterson, 1993). A distinctive quality of the teleost record is the very large number of living clades whose first appearances are recorded in the earliest Tertiary (see figs. 36.1–36.6 in Patterson, 1993).

Within actinopterygians, the vast majority of terrestrial (freshwater) fishes are members of the Ostariophysi, a major clade that includes carps, characins, suckers, loaches, and catfish. Ostariophysans have largely a Tertiary record, with a few clades either appearing and terminating in the Cretaceous (e.g., Otophysi and some *incertae sedis* Siluroidea and Characiformes) or originating in the Cretaceous and persisting to the present (e.g., Diplomystidae, Ariidae). Nonetheless, a few basal freshwater actinopterygian groups straddle the K/T boundary, a pattern evident even at the species level. These include the chondrosteans—the acinpensersids (sturgeons) and the polyodontids (paddlefish). These more primitive forms, along with the lepisosteids (gars) and amiids (bowfins), account for 7 of the 15 species of actinopterygians known from the Upper Cretaceous Hell Creek Formation of Montana (Archibald, 1996a). Remarkably, all these groups of fishes, originally the denizens of Cretaceous river systems, not only persisted through the Tertiary but are still found today in the Mississippi river drainage. The remaining eight groups of bony fishes preserved in the Hell Creek Formation are teleost clades, although the more basal actinopterygians dominate the sample of fish remains from this sequence. Wilson et al. (1992) reassigned some Hell Creek teleosts previously described as the extinct *Platacodon* as extant Esocidae. These authors also argued that the dearth of Cretaceous teleost lineages is a problem of sampling and monographic bias, and that many of the Tertiary clades probably have Mesozoic occurrences awaiting description. Revised studies of teleosts, as well as the records of basal actinopterygians noted above, underscore the geochronological endurance of many freshwater fish clades. In contrast to the marked extinction of elasmobranchs, 9 of 15 species of bony fishes

(60%) in the Hell Creek Formation persist into the Tertiary (Archibald, 1996a). Moreover, the prospects for marked improvements in documenting the Cretaceous record of teleosts argue against linking the impressive diversification of this group strictly with environmental changes that post-date the Mesozoic.

The other division of Osteichthyes, the sarcopterygians, are primarily a Paleozoic radiation with a few clades (Gnathorizidae, Ceratodontidae, Laugiidae) persisting through the Mesozoic and in some cases early Cenozoic (Shultze, 1993). Some sarcopterygian clades show remarkable longevity; these include Neoceratodontidae (Triassic to present), Latimeriidae (Jurassic to present), and Lepidosireniidae (Cretaceous to present). Many of these lineages are monotypic or contain very few taxa. The more marked sarcopterygian diversification in the Paleozoic thus gave way to a few very persistent clades whose diversity was greatly overshadowed by that of the actinopterygians.

Lissamphibians. The modern amphibian groups—frogs, salamanders, and caecilians—belong to the Lissamphibia, some of whose surviving lineages have a long fossil history (Milner, 1993). The earliest lissamphibian records, represented by the extinct Triadobatrachidae, date back to the earliest Triassic. Both frogs (Anura) and salamanders (Caudata) appear by the mid Jurassic, and some of these lineages (e.g., the anuran Discoglossidae) persist today (Estes, 1969). Many lineages of lissamphibians, some of them extant groups, have records extending back at least to the Cretaceous (Nessov, 1988). As in the case of some other vertebrate groups, the apparent restriction of a large number of lineages of frogs and salamanders to the Cenozoic may reflect sampling and monographic bias. Amphibian remains are usually fragmentary and often elude identification. Estes (1969, 1982) pioneered much of the taxonomic work on Cretaceous and Tertiary amphibians as well as squamates (see below).

As in the case of several other vertebrate groups, the primary reference sections for latest Cretaceous and earliest Tertiary lissamphibians are in western North America. Lissamphibians are less common in the Upper Cretaceous Hell Creek Formation of Montana (Archibald, 1996a) than they are in the Upper Cretaceous Lance Formation in eastern Wyoming (Estes, 1964). The faunal contrast has been attributed to more fluvial conditions in the Lance sequence (Archibald, 1996a). Of the five families of lissamphibians in the Hell Creek, only one, the Sirenidae, includes extant species. The remaining

four families, though extinct, extend into the Tertiary. In fact, all eight of the lissamphibian species identified from Hell Creek are survivors of the K/T event (Archibald, 1996a).

Testudines (turtles). Turtles are an ancient group of vertebrates whose remains of shell fragments are among the most common fossils found at many terrestrial sites. The record of the group extends back to the Triassic, but the Cretaceous is notable for marking the first appearances of many turtle lineages, several of which (Chelydridae, Pelomedusidae, Trionychidae, Cheloniidae, Carettochelyidae) survive today (Hutchison & Archibald, 1986). Virtually all other extant turtle clades date back to the Paleocene (Benton, 1993). With respect to the Cretaceous-Tertiary transition, turtles, like lissamphibians and actinopterygian fishes, show a high survival rate. Eleven higher taxa of Cretaceous turtles have records that cross the K/T boundary, while only five clades disappear before the end of the Cretaceous (fig. 39.1 in Benton, 1993). This pattern pertains to more refined, albeit more local, analyses. Fifteen of seventeen (89%) turtle species from the Cretaceous Hell Creek fauna are also known from Tertiary faunas (Archibald & Bryant, 1990; Gaffney & Meylan, 1988; Brinkman & Nicholls, 1993; Archibald, 1996a).

Squamates (lizards and snakes). The early squamate record, though spotty, is lately much improved. Inspired by important analyses by Estes (1964, 1983), recent work has expanded greatly the taxonomic treatment of Cretaceous lizards (e.g., Nessel, 1985, 1988; Richter, 1994; Gao, 1994; Gao & Fox, 1996; Gao & Hou, 1995; Cifelli & Nydam, 1995). Extremely large and diverse samples of Late Cretaceous lizards (see Novacek et al., 1994; Novacek, 1996) are now under study by Gao Keqin. Accordingly, even some of the most recent reference work on squamate geological distributions (Benton, 1993) warrant revision. At present it is apparent that the record of fossil lizards extends back at least to the Late Jurassic, but no Jurassic lizard can be referred to any of the modern clades (Seiffert, 1973; Estes, 1983).

Diversification of many of the modern lizard groups is first recorded in the Cretaceous and early Tertiary (Estes, 1983; Sullivan, 1987; Benton, 1993; Cifelli & Nydam, 1995; Gao & Fox, 1996). Recent work has pushed back the minimum age of first occurrence in several cases. For example, the Iguanidae* (* asterisks indicate a metataxon not diagnosed by apomorphies; see Gauthier et al., 1988; Estes et al., 1988), Scincidae, Xenosauridae, and Necrosauridae* have been listed as first ap-

pearing in the latest Cretaceous, Maastrichtian stage (ca. 75–65 Ma) in recent compendia (e.g., Benton, 1993). It is clear now that these clades date back at least to the preceding Campanian stage (ca. 83–80 Ma) in North America (Gao & Fox, 1996). Possibly contemporaneous occurrences of Iguanidae* and Necrosauridae* are known from Central Asia (Borsuk-Bialynicka, 1991). The extant family Anguidae is first recorded from the early Campanian of North America (Gao & Fox, 1996). Other groups of at least Campanian age include the more advanced varanoids, Varanidae and Helodermatidae, and the diverse Teiidae, although Winkler et al. (1990) identified possible teiids from the Early Cretaceous (Aptian or Albian) of Texas. Early Cretaceous occurrences are also cited for the Gekkonidae (Alifanov, 1989), a possible relative of Necrosauridae* (Cifelli & Nydam, 1995), and a scincomorph relative (?Anguidae in Winkler et al., 1990, reassigned by Gao & Fox, 1996). Notably, the extant Cordylidae, Amphisbaenidae, and Xantusiidae, listed by Benton (1993) as first appearing in the Paleocene, are now known from possibly referable taxa in the Late Cretaceous (Borsuk-Bialynicka, 1991; Gao & Fox, 1996).

Given the above-noted ranges, it is clear that many lizard higher clades survived the K/T extinction event. Of some 19 Tertiary or extant clades usually designated as families, 13 (e.g., Iguanidae*, Agamidae, Amphisbaenidae, Gekkonidae, Xantusiidae, Teiidae, Scincidae, Cordylidae, Anguidae, Xenosauridae, Necrosauridae*, Helodermatidae, and Varanidae) have first occurrences in the Cretaceous. Nonetheless, selective extinction is apparent at lower taxonomic levels. For example, teiids, the most diverse group of Late Cretaceous lizards in both North American and Asian faunas (Estes, 1983; Borsuk-Bialynicka, 1991; Gao & Fox, 1996) show marked extinction at the K/T boundary. All four species of teiids from the Hell Creek Formation are not known above the boundary (Archibald, 1996a). [Before the end of the Cretaceous, teiids likely entered South America and later diversified there during the Tertiary (Gao & Fox, 1996).] In fact, only three of the ten lizard species assigned to seven different families persist into the Tertiary (Archibald, 1996a). This pattern should be tested against records in the Gobi Desert of Mongolia and northern China, where Late Cretaceous lizard faunas are even more diverse and much better preserved than in North America. Unfortunately, an Upper Cretaceous-Lower Paleocene sequence preserving the K/T boundary has yet to be found in the Gobi (Novacek et al., 1994).

This improving document of lizard distributions

does not, unfortunately, extend to its squamate sister taxon, the snakes (Serpentes). Snakes have a record extending back to the Early Cretaceous, and several of the extant or Tertiary higher clades (Aniliidae, Boidae, Madtsoiidae) have occurrences in the Late Cretaceous (Benton, 1993). The emergence and impressive diversification of some of the more modern groups, like Colubridae, Viperidae, and Elapidae, are currently restricted to the Tertiary. Doubtless, occurrences of snakes in the Cretaceous record will increase when the fragmentary squamate remains from many collections receive more expert study.

Champsosaurs. The crocodile-like appearance of the champsosaurs is misleading, as this group, also denoted choristoderans, lies outside crocodilians and their archosaur relatives, the dinosaurs (including birds) and pterosaurs. The group ranges at least from the Early Cretaceous to the middle Eocene (see summary in Benton, 1993). Champsosaurs are very common, if fragmentary, fossils in Late Cretaceous and early Tertiary faunas. Archibald and Bryant (1990) and Archibald (1996a) claimed that *Champsosaurus* straddled the K/T boundary, but the lack of a comprehensive classification precludes any analysis of distributions for species of this taxon.

Crocodiles. The impressive and enduring fossil record of crocodilians extends from the Middle Triassic to the present. Appreciable radiations of lineages are recorded in the Late Jurassic, the middle to Late Cretaceous, and the early Tertiary. Five out of nine higher clades that have Tertiary or Recent records are known from the Cretaceous (Benton, 1993). This includes the earliest occurrences of the extant "families" Alligatoridae and Crocodylidae. On the other hand, several crocodilian higher clades (Baurusichidae, Peirosauridae, Hsisosuchidae, Paralligatoridae, and Dolichochampsidae) disappear at or slightly earlier than the K/T boundary. Species-level analysis in the Hell Creek-Tullock Formation section shows that four of the five crocodilian species from the Hell Creek Formation extend into the Paleocene (Archibald, 1996a).

Non-avian dinosaurs. Dinosaurs, long the subject of intense and unabated scientific and popular interest, have in more recent years been the focus of massive systematic revision (e.g., Weishampel et al., 1990; Sereno, 1997). Such studies apply cladistic methods adopted earlier in the case of many other vertebrate groups. In addition, there has been a great surge during the last decade of discoveries of dinosaur fossils worldwide. Both field discoveries

and modern systematic treatment allow revisions and refinement of the dinosaur record and a scrutiny of numerous theories on dinosaur evolution (Currie & Padian, 1997).

One evolutionary scenario of particular relevance here is the correlation between the Late Mesozoic radiation of herbivorous hadrosaurs, ankylosaurs, and ceratopsians and the emergence of the angiosperm flora (Weishampel & Norman, 1989). This scenario was derived partly from the observation that Cretaceous tetrapod faunas showed pronounced differences between Northern and Southern Hemispheres. In the north (but primarily the North American record—see comments below) there is an apparent decrease during the Cretaceous of high-browsing sauropods (Weishampel & Norman, 1989) and stegosaurs, but a concomitant increase and diversification of ankylosaurs (Maryánská, 1977; Coombs, 1978), ornithopods (Weishampel & Norman, 1989; Sereno, 1997), and especially ceratopsians. Radiation of the latter began with Psittacosauridae in the Early Cretaceous (Sereno, 1997), and later with protoceratopsids in East Asia and North America (Russell, 1970; Maryánská & Osmólska, 1975) and huge ceratopsians in the latest Cretaceous of North America (Sereno, 1997). In the Southern Hemisphere, sauropods continued to dominate and hadrosaurid ornithopods remained rare throughout the Cretaceous (Bonaparte, 1987). Pachycephalosaurids also appeared in the Early Cretaceous (Maryánská & Osmólska, 1974; Sues & Galton, 1987) and diversified throughout the period, especially in central Asia and western North America (Sereno, 1997).

This increase in relative abundance and diversity of two groups of large herbivores—the hadrosaurid ornithopods and ceratopsid ceratopsians—has been claimed to track the increase in relative abundance and diversity of angiosperms in disturbed areas (Bakker, 1978; Wing & Tiffney, 1987; Weishampel & Norman, 1989). These groups probably foraged in herds, with the effect of considerable harvest on foliage dominated by "weedy" angiosperms. Accordingly, this interaction represents a putative case of coevolution where low-browsing herbivorous dinosaurs set up conditions for favorable selection of weedy foliage, typical of angiosperms (Bakker, 1978). Under this scheme, South American Late Cretaceous plant floras, where high-browsing sauropods continued to flourish, should differ significantly from contemporaneous North American vegetation. Namely, disturbed angiosperm-dominated vegetation should show low abundance and diversity (see discussion in Wing & Sues, 1992). There is some evidence to

suggest that the diversification of angiosperms in higher southern latitudes was slower, at least up until Cenomanian times (Drinnan & Crane, 1990). Nonetheless, the correlation between the diversification of low-browsing herbivorous dinosaurs and angiosperms is biased toward the North American record. Indeed, it is difficult to draw the contrast between simply the Northern and Southern Hemispheres. High-browsing sauropods, for example, continued to flourish alongside hadrosaurs and ankylosaurs in the Late Cretaceous in Mongolia and China, where there is also evidence for angiosperm assemblages (Gradzinski et al., 1977; Novacek, 1996). Sauropods, and for that matter hadrosaurs, are very rare, however, in Upper Cretaceous red bed sequences of central Asia that represent semi-arid or desert conditions. Here protoceratopsians and ankylosaurs are found in abundance (Gradzinski et al., 1977; Jerzykiewicz et al., 1993; Novacek et al., 1994). Unfortunately, the rich concentrations of vertebrate fossils in these red-bed facies are not accompanied by adequate concentrations of plants and pollen. One might be forced to the conclusion that a rough correlation between the relative dominance of certain dinosaur taxa and more open-habitat, angiosperm-dominated vegetation typified local conditions and intervals but not necessarily global-scale patterns.

One aspect of the non-avian dinosaur record is of course incontrovertible: there is no unambiguous evidence of dinosaur occurrence in Tertiary sequences anywhere in the world, and dinosaur extinction at the end of the Mesozoic is one of the famous hallmarks of the fossil record. Two issues concerning this record, however, must be considered. First, there is an uneasy reliance on the North American record for calibrating the dinosaur extinction event. Although Late Cretaceous dinosaur faunas are well documented in numerous localities on most continents, latest Cretaceous dinosaurs—namely, occurrences just below the K/T boundary—are virtually confined to localities in western North America (Archibald, 1996a). The only possible exceptions to this isolated record are controversial latest Cretaceous occurrences in China and South America (see Archibald, 1996a). This dearth of global-scale data still leaves open the possibility that dinosaurs may have persisted into the Paleocene, or alternatively may have disappeared before the end of the Cretaceous, in some regions of the world.

A second and related issue concerns the tempo and timing of dinosaur extinction. It is clear that the K/T boundary in North America shows the abrupt termination of notable dinosaurs, such as

Tyrannosaurus and *Triceratops*, but there is an argument that dinosaur diversity was on the wane for several million years preceding the end of the Cretaceous (see Archibald, 1996a). This is based on documentation of North American assemblages distributed between Judithian and Lancian Land Mammal Ages (75 Ma to 65 Ma), showing a reduction in dinosaur (primarily ceratopsian and hadrosaurid) diversity from 33 genera (Weishampel, 1990) to 19 genera (Archibald & Clemens, 1982). Russell's (1984) counterclaim that Lancian dinosaur diversity was maintained above the level of 30 genera has been disputed by Archibald (1996a) because many of the critical taxa from the Lancian have not received published descriptions, and Russell's rarefaction analysis introduced incorrect assumptions concerning sample sizes. Archibald (1996a: 37) concluded: "This means for the best, and really only well-sampled, latest Cretaceous dinosaur faunas in the world, the fossils themselves reveal a 40% decline in genera of dinosaurs in the waning ten million years of the Cretaceous. The dinosaurs were indeed on a slippery slope of decline long before the K/T boundary."

Despite such a generalization about dinosaur decline, many ambiguities concerning the relevant record persist. Archibald (1977) and others noted a 10-foot gap between the uppermost occurrence of dinosaur bones in the Hell Creek Formation and the K/T pollen shift and iridium layer. In the more southern localities of New Mexico, dinosaur fossils were found three to six feet—and trackways 15 inches—below the layer with iridium concentrations (Pillmore et al., 1994). These observations might be taken to dispute the firm coincidence between dinosaur extinction and the asteroid event. However, Archibald (1996a) noted that the uppermost section of the Hell Creek Formation is generally depauperate in fossil vertebrates, and the apparent gap between the last dinosaur occurrences and the iridium layer could be a function of samples denuded by leaching of bone, low rates of sediment accumulation, and soil development unfavorable to preservation. Other attempts to document dinosaur diversity and distribution through this critical section include work by Sheehan et al. (1991), who claim to record steady numbers of individuals and taxa of dinosaurs through the Hell Creek. This analysis, however, focused on family-level taxa, where the disappearance of genera or species would not be recorded. At the present time, it seems reasonable to claim that there is some indication of decline in dinosaur generic diversity over the last ten million years of the Cretaceous, at least in selected areas of western North America,

but finer-scale patterns bearing on dinosaur diversity approaching the K/T boundary are unclear.

Avian dinosaurs (birds). Birds as well as other dinosaurs have enjoyed a recent wave of paleontological discovery and monographic study, resulting in a much improved picture of their early history and phylogeny (Gauthier, 1986; Chiappe, 1992, 1995; Padian & Chiappe, 1998a, b). Although bird specimens from the Mesozoic are still comparatively rare, they include some of the most exquisitely preserved and important fossils from the Mesozoic record. That assemblage includes *Archaeopteryx lithographica* from the Upper Jurassic Solenhofen limestones, still the earliest and most basal member of birds (Padian & Chiappe, 1998a). These spectacular fossils are augmented by skeletons, many of which have been found only in recent years, of a variety of Cretaceous birds. Argentina, Spain, and China have produced the short-winged enantiornithines, which vary from the sparrow-sized *Sinornis* to the turkey vulture-sized *Enantiornis*. Cretaceous sequences of Patagonian Argentina have yielded the flightless *Patagopteryx*, and the Upper Cretaceous of North America preserves skeletons of the flightless loon-like *Hesperornis*, and the tern-sized *Ichthyornis* (Chiappe, 1995). A particularly spectacular addition to this sample is represented by new finely preserved skeletons with feather impressions of both non-avian theropods (*Sinosauropteryx*, *Protarchaeopteryx*) and birds from the Liaoning Province of China, an assemblage dated as Late Jurassic or Early Cretaceous (Padian & Chiappe, 1998a). Other recent discoveries include the flightless bird *Mononykus* from the Late Cretaceous of Mongolia (Chiappe et al., 1998), a form that shows a suite of features common to both more modern birds and non-avian maniraptoran theropods. Fossil evidence extends to embryos and eggs of the Late Cretaceous form *Gobipteryx* (Elzanowski, 1995) as well as a nestling enantiornithine bird from the Lower Cretaceous of Spain (Sanz et al., 1997).

The dramatic influx of new information on Mesozoic birds does not radically alter a primary aspect of the avian fossil record. The diverse lineages of modern and extant bird lineages are overwhelmingly restricted to the Tertiary (see compilation in Unwin, 1993). The Mesozoic bird groups noted above do much to elucidate the close affinities and transitions between birds and other theropod dinosaurs (though this theory has a few detractors; see Martin, 1991; Tarsitano, 1991; and Feduccia & Wild, 1993), but they cannot be placed within the crown-group (neornithines) that contains all extant birds and their common ancestor. Instead, these

Mesozoic stem lineages, primarily the Enantiornithes, *Patagopteryx*, and Ornithurae, fail to survive into the Tertiary (Padian & Chiappe, 1998b). Conversely, few extant higher taxa (orders) of birds, and no extant families, are known from the Cretaceous. The putative Mesozoic candidates include Charadriiformes and Procellariiformes from the latest Cretaceous of Wyoming and New Jersey (Olson, 1985), possible neornithines from the Late Cretaceous of Canada (Tokaryk & James, 1989), Gaviiformes from the Late Cretaceous of Antarctica and Chile (Chatterjee, 1989; Olson, 1992), and Anseriformes from the Late Cretaceous of Antarctica (Noriega & Tambussi, 1995). In addition, some fragmentary Cretaceous remains of possible neornithines have been recovered from Europe and Asia (Nesov & Jarkov, 1989, 1992; Hou & Liu, 1984; Kurochkin, 1988). In contrast, the early Tertiary shows abundant, though often fragmentary, evidence of the radiation of modern birds. Virtually all of the 35 or so extant avian orders, with the possible exception of the speciose passeriformes, were present by the Eocene (Unwin, 1993; Feduccia, 1995).

This gap between the ranges of stem Mesozoic birds and modern bird lineages has prompted the view that the latter underwent an explosive radiation over a 5-to-10-million-year period during the early Tertiary (Feduccia, 1995). This pattern suggests a latest Cretaceous demise of more archaic lineages, a subsequent bottleneck in bird diversity, and a dramatic reorganization and diversification of bird lineages a few million years after the Cretaceous extinction event. The origins of extant orders, families, and then genera are claimed to track the temporal cascade often applied to Cenozoic mammals (Feduccia, 1995). Others (e.g., Padian & Chiappe, 1998b) have argued that this is an overinterpretation of a spotty fossil record which may, over time, reveal abundant and unambiguous evidence of Cretaceous neornithines. Moreover, comparisons of gene differences among neornithine bird orders that assume clock-like rates of molecular evolution have been interpreted to indicate a time span of 90–100 million years (Hedges et al., 1996) or even earlier (Cooper & Penny, 1997) for the divergence of these lineages. Thus, both a skepticism concerning the quality of the Cretaceous bird record and a reliance on extrapolations based on gene comparisons might lead one to argue that the radiation of modern birds began in the late Mesozoic and persisted through the K/T extinction event with minimal disruption. An attractive feature of this scenario is the obvious synchrony between divergence of major bird clades and the marked con-

tinental fragmentation and isolation that characterized the Cretaceous (Hedges et al., 1996).

Which of these alternative hypotheses for the origin and timing of the modern bird lineages seems more persuasive? One might argue that both the implications of the molecular evidence and the expectations for the fossil record (it always gets better, with revelations of older fossils) provide a strong rationale for a Late Mesozoic radiation of these groups. It is, however, difficult to leap to this conclusion; divergence dates based on assumptions of clock-like rates in genes have been the subject of much skepticism that reflects observations of varying rates among many lineages. With respect to the paleontological data, it is noteworthy that the markedly improved record for Mesozoic birds includes extremely well-preserved fossils of avian stem taxa, but no comparable evidence for modern groups. Many of these stem taxa are small delicate forms, no less vulnerable to damage or loss in preservation than are various neornithines. Furthermore, phylogenetic analysis that might predict an earlier occurrence of some Cenozoic bird lineages based on the known fossil range of their nearest sister taxa (Norell, 1992; Norell & Novacek, 1992) cannot be readily applied here. This is because all the well-represented Mesozoic forms are basal to the more modern lineages, and the relationships among the extant clades are very poorly resolved. The only Cretaceous neornithine forms, as noted above, are fragmentary, and their affinities with particular members of the modern bird orders are not readily identifiable. Thus, although it may be tempting to extend the divergence of more modern lineages well into the Cretaceous, this is not clearly indicated by the fossil record. What is known of that record and the higher-level phylogenetic relationships of birds fails to refute the notion that the explosive radiation of modern bird lineages largely occurred after the K/T extinction event.

Given the above-noted uncertainties in the early fossil record of birds, one might expect that finer-scale patterns across the K/T boundary are even more elusive. Studies of vertebrates in the Cretaceous Hell Creek-Paleocene Tullock sequence included only 30 specimens representing only four bird species (Bryant, 1989). The scanty sample precluded any kind of range analysis comparable to those described for most other terrestrial vertebrate groups in the local section (Archibald & Bryant, 1990). Little with respect to bird distribution during the Late Cretaceous-early Paleocene interval can be ventured except for the observation that the best represented group of Cretaceous birds, the enantiornithines, do not survive the end of the Creta-

ceous. Extinction of this basal bird group by the end of the Cretaceous is in fact agreed upon by authors who argue for either a Cretaceous (Chiappe, 1995) or a Cenozoic (Feduccia, 1995) radiation of the modern bird lineages.

Mammals. Of all the groups of terrestrial fossil vertebrates, the mammals perhaps offer the most sensitive picture of faunal transitions during the Cretaceous-early Tertiary. While the fossil record for mammals during this interval is inconsistent, it is much enriched and much studied compared to data on other vertebrate groups. Mammals are known from diverse lineages on either side of the K/T boundary (Fig. 7). Apparent patterns of mammalian distribution are not so easily ascribed to biases due to an impoverished record, as they might be for birds, amphibians, or other groups. Moreover, mammals themselves show a dramatic evolutionary reorganization that has been critical to describing and subdividing the whole of the Cenozoic. Finally, it is clear that mammals represent the primary successors to the non-avian dinosaurs as the dominant terrestrial megafauna in the evolving Cenozoic ecosystems.

Stem mammal groups first appear in the fossil record 210 million years ago, during the Late Triassic (see review in Rougier & Novacek, 1998). Diversification during the Jurassic involved several major lineages primarily represented by fragmentary teeth and jaws in isolated localities in Europe, western North America, South Africa, and Asia. By the Early Cretaceous, several basal clades are represented (Stucky & McKenna, 1993; McKenna & Bell, 1997): triconodonts, symmetrodonts, cladotheres (amphitheriids, dryolestids, and other groups), and herbivorous multituberculates, as well as a number of *incertae sedis* taxa (e.g., docodontids). The extant monotremes (duck-billed platypus and echidna) are doubtless very primitive mammals that shared an early history with the many Mesozoic groups. The Cretaceous occurrence of monotremes, however, was not revealed by fossils from Australia until recent years (Archer et al., 1985). Early Cretaceous faunas also include the first allies of the more modern Theria, the group comprising living marsupials and placentals (Kielan-Jaworowska & Dashzeveg, 1989; Cifelli, 1993b). The most intriguing, and controversial, record for an Early Cretaceous therian is claimed for Australia, where a jaw with cheek teeth described as *Ausktribosphenos* is identified as a basal placental mammal (Rich et al., 1997). However, this allocation is widely questioned, as *Ausktribosphenos* seems more likely an archaic mammal with some similarities to the cheek

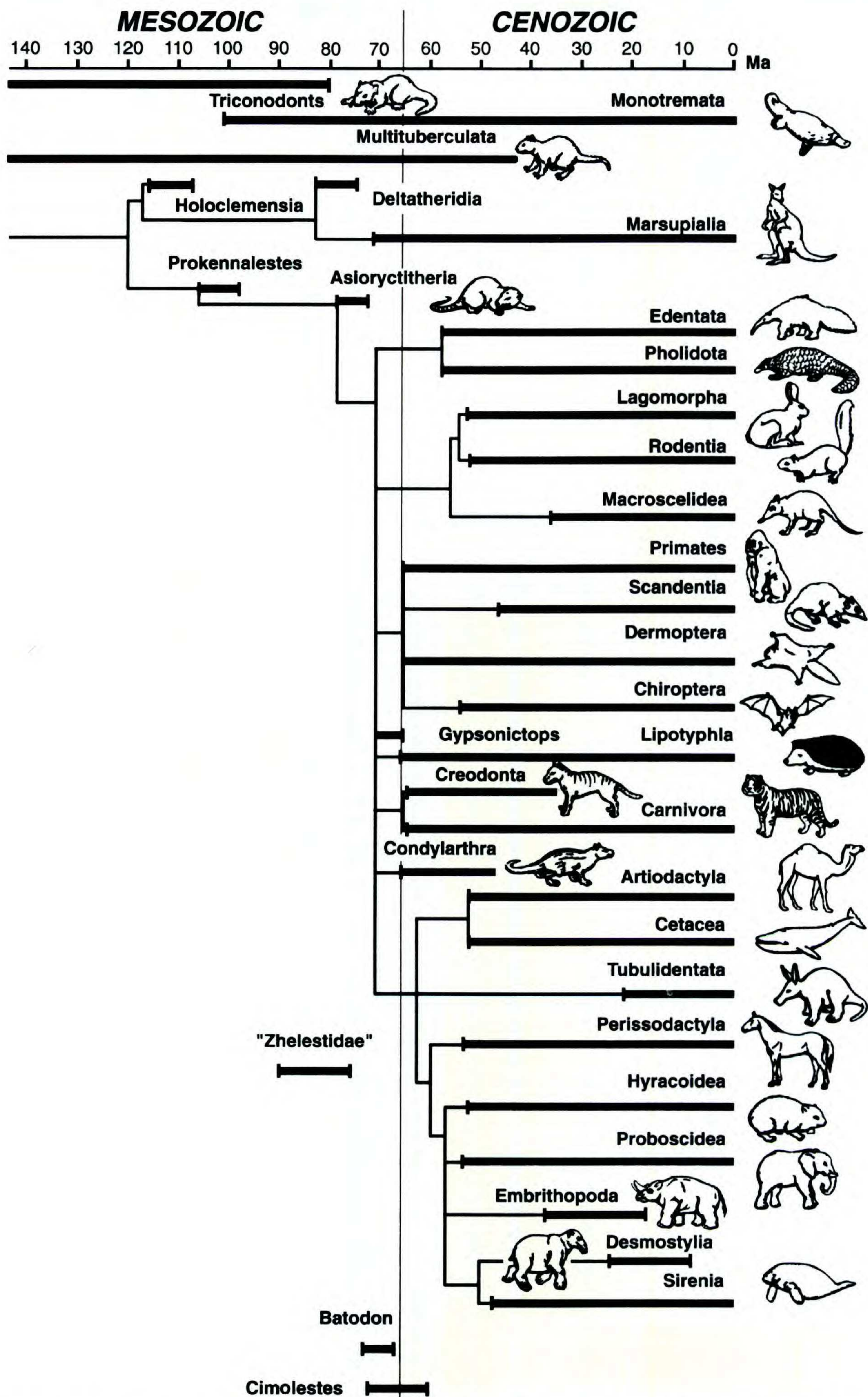


Figure 7. Relationships (thin lines) and geochronological ranges (horizontal bars) for major clades of therians and selected other mammals. Thin lines also depict ghost lineages necessary to calibrate the age of origin of a given taxon based on the known age of its nearest sister taxon. Internodal distances are slightly exaggerated to represent the resolution among clades.

tooth anatomy of more modern placentals (Wue-trich, 1997; Rougier & Novacek, 1998).

Later Cretaceous mammalian faunas mark the appearance of more advanced therians and the diversification of more basal forms such as the multituberculates. Although most of the literature of Late Cretaceous mammals is concentrated on the less complete jaws and teeth representing many taxa from North American sequences (Clemens, 1966, 1973; Clemens & Kielan-Jaworowska, 1979; Lillegraven, 1969; Lillegraven & McKenna, 1986; Fox, 1984; Cifelli, 1990, 1993a; Archibald, 1996a), that record has been greatly enhanced by a dramatic array of complete skeletons and skulls representing Late Cretaceous therians and multituberculates from Mongolia (Gregory & Simpson, 1926; Kielan-Jaworowska, 1974, 1992; Novacek et al., 1994, 1997; Dashzeveg et al., 1995; Rougier et al., 1996, 1997; Rougier & Novacek, 1998). Later Cretaceous faunas from Uzbekistan now are known to include a diversity of zhelestids, mammals known only from rather broad molars that suggest herbivorous habits and possible phylogenetic affinities with the extant ungulate placentals (Archibald, 1996b). Late Cretaceous mammal assemblages from South America are highly endemic, as indicated by *Gondwanatherium* (Bonaparte, 1987, 1990) and other nontherian taxa. Gondwanatheres have recently been discovered in the Cretaceous of Madagascar (Krause et al., 1997).

Mammalian diversity during the Mesozoic reflects a variety of ecological roles. These include insectivorous and carnivorous forms (e.g., symmetrodonts, deltatheridians, and asioryctitheres) as well as the herbivorous multituberculates. The latter show an interesting parallel to the placental order Rodentia in having dentitions suited for fruit and seed eating. Multituberculates lack any affinity with rodents; they also appear some 100 million years before the first occurrence of rodents (Novacek, 1997). Nonetheless, because of their specialized dentitions and skulls, multituberculates are commonly labeled as the ecological equivalent to the rodents. Multituberculates also compare with extant rodents in their relative diversity and abundance in fossil assemblages. A very rich Late Cretaceous assemblage from Mongolia (Dashzeveg et al., 1995) has yielded more than 800 skulls of fossil mammals, of which at least 80% represent several species of multituberculates. This dominance of small herbivorous forms resembles the high proportion of rodent species in many extant habitats that support small mammals (Dashzeveg et al., 1995). The basic trophic organization of Cretaceous small mammal communities thus foreshadowed ro-

dent-dominated communities during the Cenozoic, even though Cretaceous communities comprised much fewer species and the transition involved dramatic taxonomic turnover. Various groups of Mesozoic mammals show locomotory specializations relating to burrowing (multituberculates) or even hopping (zalambdalestid therians). Despite this heterogeneity in form and inferred habit, Mesozoic mammals are rather stereotypic for at least one quality: none of them were very large. In fact, the average estimated body mass for 29 species of Late Cretaceous mammals is 150 g, in contrast to the average mass of 1.01 kg for 33 mammal species (27 of them new) occurring only one million years after the K/T event (Alroy, 1998). This extraordinary size increase for mammalian lineages in the Cenozoic has of course been associated with the opportunities that emerged in terrestrial ecosystems in the absence of competition from other large species, such as dinosaurs.

Subsequent to the K/T event, mammals increased not only in terms of body mass but also in diversity. In western North America, mammalian diversity rose from 20 to 45 genera within 250,000 years of the K/T event, and reached 70 genera 2 million years into the Paleocene (Archibald, 1983). The fossil record provides an incontrovertible picture of the early Tertiary radiation of mammals. Nonetheless, a central question concerning this transition remains. Is this radiation largely a phenomenon that post-dates the Mesozoic, or does it extend back to the Late Cretaceous or even earlier times? In the local Cretaceous Hell Creek-Paleocene Tullock sequence, the picture of mammalian survival across the K/T boundary is heterogeneous (Archibald & Bryant, 1990; Archibald, 1996a). Only 9% of the marsupial species survive the K/T event, whereas 50% of the multituberculates and 100% of eutherians (the group that includes the living placental orders) manage to make it through the boundary. This suggests a nascent development of the radiation of at least eutherians back as far as the Late Cretaceous. Other estimates point to even more dramatic Cretaceous diversification of the modern groups. Similar gene studies as applied to birds suggest a window of divergence of 90–100 million years for the major clades (orders) of marsupials and placentals (Hedges et al., 1996; Kumar & Hedges, 1998). Analyses sensitive to phylogenetic relationships and the age of sister taxa also suggest a Cretaceous radiation of the major clades of more modern mammals (Norell, 1992). Complementary evidence comes from the fossils themselves, as forms representing sister taxa to extant marsupials on the one hand and extant placentals

on the other are known from Early Cretaceous assemblages (Kielan-Jaworowska & Dashzeveg, 1989; Cifelli, 1993b). Finally, if ungulate affinities of the later Cretaceous zhelestids are accepted, there is even evidence for a subclade of placentals that predates the Cenozoic.

This combination of evidence and assertion fails, however, to firmly establish the greater antiquity of the radiation of the extant therian clades. As in the case of birds, the Mesozoic therians are virtually all stem taxa: they are related to but outside of the crown-groups representing extant marsupials and placentals (Fig. 7). In fact, Cretaceous Mongolian forms like *Kennalestes*, *Asioryctes*, and *Zalambdalestes*, taxa long thought to be intimately associated with placental insectivorans, are now known to preserve features that suggest their basal position relative to all placentals and their last common ancestor (Novacek et al., 1997). Likewise, well-represented metatherians from the Cretaceous of Mongolia are excluded from the group that includes extant marsupials and their common ancestor (Rougier et al., 1998). As for the Late Cretaceous North American therians, the limited evidence provided by dentitions and isolated teeth frustrates any unambiguous assignment to a modern placental or marsupial clade. There is nothing known about the dental anatomy of these forms that would allow one to claim they were members of either of the two therian crown-groups, even though certain species of these Cretaceous lineages survived the K/T event. The major contradiction here is the Cretaceous Zhelestidae (Archibald, 1996b), but again the limited evidence of dentitions prevents their confident assignment or even close alliance with some placental ungulate clade. Given the dramatically enriched sampling of Cretaceous mammalian faunas (there is no Paleocene mammal assemblage better represented by diverse and abundant skulls and skeletons than the Upper Cretaceous assemblage from Ukhaa Tolgod in Mongolia; see Dashzeveg et al., 1995; Novacek, 1996), it is surprising that bona fide lineages of placentals and marsupials have not yet been discovered. Indeed, here it is more difficult to argue, as in the case of birds, that the Cretaceous record is simply too impoverished to turn up these forms. The available evidence suggests that diversification of the therian clade is rooted in the Cretaceous, but does not refute the more traditional view that the intense pulse of radiation of the more modern placental and marsupial subclades took place in the early Tertiary.

During the early Paleocene, many of the smaller mammal lineages had enlarged, elaborated incisors,

canine, and premolars, suggesting diversification and refinement of diets for fruits, seeds, and small prey. More robust forms were squat, heavy-legged creatures such as pantodonts with generalized dentitions suitable for mashing vegetation, but virtually none of these Paleocene mammals were specialized browsers (Stucky, 1990). The Paleocene/Eocene transition shows significant turnover involving the replacement of archaic groups by more modern forms (Rose, 1981, 1984; Stucky, 1990). The more modern herbivores (those with extant members) first occur at the Paleocene/Eocene boundary, including rodents at the end of the Paleocene. Major biotic interchange in the Northern Hemisphere during the early Eocene resulted in marked homogenization of the mammalian faunas (McKenna, 1983; Flynn, 1986). The dominant modern ungulates, the even-toed artiodactyls (camels, hippos, antelope, bovines, and others) and the odd-toed perissodactyls (horses, rhinos, tapirs, and some extinct lineages), appeared in the Northern Hemisphere at the beginning of the Eocene. Diversification of these forms in the early Eocene also involved a trend to larger body size (Rose, 1984; Stucky, 1990).

The highest alpha-level diversity in mammals was reached in the late Paleocene and early-middle Eocene. Thereafter, a decrease in diversity and more dominance of certain keystone species abides. This clumped distribution of species seems characteristic of more open habitats, which expanded during the cooling phase in the later Eocene-early Oligocene interval (Stucky, 1990). The late Eocene shift toward more open savanna-like habitats with plants of lower stature (Wing, 1987) was accompanied by evolution in plant-eating mammal lineages of larger body size, increased lophodonty, emphasis of cursorial features, and a decline in arboreal forms (Webb, 1977; Stucky, 1990; Wing & Sues, 1992). This coincidence in fauna and floral trends suggests coevolution and perhaps a reprise of the dinosaur-angiosperm interdependence in the Cretaceous. More open vegetation caused by increased seasonality certainly favored diversification of large, wide-ranging grazers and browsers. These animals likely reciprocated in maintaining vegetation at levels that favored the diversification and increased abundance of weedy plants, particularly herbaceous angiosperms (Wing & Tiffney, 1987).

DISCUSSION AND CONCLUSIONS

The foregoing summaries of the vertebrate record, as well as the brief synopsis of related geographic, climatic, floral, and non-vertebrate faunal trends, provide a matrix for a few generalizations

concerning the crucial Cretaceous-early Tertiary interval. Clearly this interval is among the best sampled within the Phanerozoic for terrestrial ecosystems, with a picture that is rapidly improving. Nonetheless, several persistent issues, such as those relating to the source and specific impact of Cretaceous extinction, the disparity between fossil occurrences and extrapolations for the time of origin of some key modern groups, and the relationship between local events and global-scale patterns have not been completely resolved by the recent accumulation of fossil data. Below are a few of the principal issues that relate to the evidence reviewed herein.

EARLY CRETACEOUS ORIGINS OF THE MODERN TERRESTRIAL ECOSYSTEM

There seems little doubt that the Early Cretaceous was the crucial time of origin for a terrestrial ecosystem that forecast the environments persisting today. The primary representatives of this dramatic shift are the angiosperms and the insects (especially the pollinating forms). Despite some argument for a lag between these components, their broad coincidence in appearance and diversification seems well established (Grimaldi, 1999), a logical reflection of the ecological interdependence of these components. The question remains as to whether any of the vertebrate groups show changes that reinforce the sweeping transformations indicated by plants and non-vertebrate groups. As summarized above, most vertebrate groups for which an adequate fossil record is available show moderate or marked turnover between the Late Jurassic and Early Cretaceous. Nonetheless, it is difficult to argue that these changes were very different in scope and magnitude from the frequent cycles of turnover throughout the Mesozoic and were directly related to the emergence of an angiosperm-dominated flora. The most notable proposal for a coevolutionary relationship concerns the coincidence of angiosperm diversification and the replacement of high-browsing herbivores (e.g., sauropods) by lower-browsing forms (notably ceratopsians and hadrosaurs) in the Cretaceous (Weishampel & Norman, 1989). The argument depends on the logical inference that low-browsing forms had an impact on vegetation that opened opportunities for weedy and woody foliage typified by angiosperms. The problem with this correlation is its uncertain scope. Although the shift in dinosaur faunal composition is clearly seen in North America, this is not so clearly demonstrated elsewhere. In fact, certain regions, such as central Asia, show a persistence of sauropods combined

with less dramatic diversification of ceratopsians throughout the later Cretaceous (Gradzinski et al., 1977; Novacek, 1996). It is then uncertain whether the angiosperm radiation worldwide can be intimately associated with dinosaur transitions recognized in some regions. Part of the problem of course is the lack of an adequate record and sampling of both fossil plants and vertebrates at many of the key Cretaceous localities. Increased emphasis on pollen sampling and study at well-known vertebrate sites would be a contribution here.

Another event that may have coincided with the Early Cretaceous angiosperm radiation was the diversification of several groups of vertebrates, namely, lizards (and snakes), therian mammals, and birds. In this way, the modern ecosystem that emerged and endured the K/T extinction event would have comprised several vertebrate groups as well as flora and non-vertebrate fauna. The appeal of this scenario also stems from the alleged coincidence between the diversification of modern groups (with extant representatives) and the patterns of biogeographic isolation and continental fragmentation that so characterized the Cretaceous (Hedges et al., 1996). The fossil record, however, fails to offer compelling evidence that indicates an Early to middle Cretaceous radiation for these modern groups. Although some advanced lizard groups are known from the Early Cretaceous, the majority of the families are not recorded until the Late Cretaceous. The Mesozoic record for modern groups of birds and mammals is even sketchier. Virtually all the better represented taxa (those preserved as skulls and skeletons) of either group are stem lineages that lie outside their respective crown-groups. The putative Cretaceous candidates for membership within modern lineage of birds are limited and represented by fragmentary evidence (see Padian & Chiappe, 1998b, and comments above). It cannot be distinguished whether many of these forms are actually members within the lineages or are sister taxa to the groups containing the common ancestor of the extant forms. Moreover, the lack of higher-level resolution among the modern bird clades compromises more precise resolution of the affinities of these Cretaceous forms.

These problems echo the situation with mammals, except the evidence for modern placentals and marsupials is perhaps even less certain, being represented largely by fragmentary dentitions from the Late Cretaceous of North America and west-central Asia. Extending groups farther back based on the geometry of their phylogenetic relationships (Norell, 1992; Norell & Novacek, 1992) does not effectively alter the pattern, because, as noted

above, Cretaceous taxa formerly thought to belong to the crown-group placentals are now recognized as stem-group taxa (Novacek et al., 1997). Thus, a discrepancy persists between the fossil evidence at hand and an attractive theory for an Early or middle Cretaceous radiation of several modern vertebrate groups. At present, it is realistic to recognize that vertebrates do not show patterns of distribution, relative abundance, and diversity that can be readily matched with the rise of the modern flora in the Cretaceous. The only exception here seems to be the proposed correlation between the angiosperm radiation and the turnover of certain dinosaur taxa, which can only be invoked in some regional situations.

CRETACEOUS-TERTIARY (K/T) EXTINCTION EVENT— TIMING AND BIOTIC IMPACTS

It is now confirmed that a major asteroid impact—as indicated by a marked spike in iridium as well as evidence of major crustal disruption in the Caribbean region—occurred 65 million years ago, at the time of the end of the Cretaceous extinction event. Moreover, it is widely believed that the impact of the bolide, drastic devastation of some of the fauna and flora, and subsequent appearance of successional vegetation were causally related, at least in the case of the record from western North America (Wing & Sues, 1992). We must nonetheless recognize the geographic limitations of the evidence for terrestrial vertebrate faunal change at the K/T boundary. As noted above, the only definitive latest Cretaceous-earliest Tertiary interval for terrestrial vertebrates is confined to western North America (Archibald, 1996a). Patterns outside this region for turnover at lower taxonomic levels are highly uncertain. Indeed, one cannot even confidently assert that non-avian dinosaurs failed to survive the K/T extinction event, at least for a very brief interval, outside western North America. In this regard, it is noteworthy that the taxonomic composition of certain floras outside North America are not drastically transformed from the Late Cretaceous to the Paleocene (Saito et al., 1986; Raine, 1988; Askin, 1988; and discussion above). Over a broader interval, of course, the absence of dinosaurs in Paleocene faunas worldwide is readily demonstrable.

Despite the magnitude of the Cretaceous-Tertiary (K/T) extinction event and its obvious impacts on non-avian dinosaurs, the extinction of vertebrates across the K/T boundary is strikingly selective. Indeed it is the marine and not the terrestrial record that shows a comprehensive level of biotic trans-

formation (e.g., see Smith & Jeffrey, 1998). Recent compilations (Archibald & Bryant, 1990; Archibald, 1996a) show that just five groups—sharks and their relatives, marsupials, lizards, and non-avian dinosaurs—suffered complete or more than 75% species extinction in the local section represented by the uppermost Cretaceous Hell Creek Formation and the lowermost Paleocene Tullock Formation in Montana. In contrast, species survival of actinopterygians (ray-finned fishes), multituberculate mammals, eutherian mammals, turtles, champsosaurs, and crocodiles across the K/T boundary ranges between 50 and 100%. Despite the strong evidence for extraterrestrial impact coincident with the K/T extinction event, these heterogeneous extinction patterns still elude satisfactory explanation (see Archibald, 1996a).

When we move beyond the fine-scale documentation unique to sections in North America, we can still recognize a striking mosaic of extinction and survival for higher-vertebrate taxa. The above summary and update of relevant records, clearly show that as many as 13 modern lizard families appearing in the Cretaceous survived across the K/T boundary. Other such enduring taxa include acin-penserids (sturgeons), polyodontids (paddlefish), lepisosteids (gars), amiids (bowfins), neoceratodontids, latimeriids, lepidosirenids, discoglossid frogs, many turtle lineages (Chelydridae, Pelomedusiidae, Trionychidae, Cheloniidae, and Carettochelyidae first occur in the Cretaceous but several surviving groups date back earlier), champsosaurs, alligatorids and crocodylids, multituberculate mammals, and selected therian mammal groups.

This impressive list of survivors of course has one exception. Dinosaurs, including a number of Cretaceous bird lineages (Padian & Chiappe, 1998b), remain the higher-level terrestrial vertebrate taxon most affected by K/T extinction. Theories for this distinction are many and varied (see Archibald, 1996a). The large size of many dinosaur taxa does not explain their particular vulnerability, as the K/T boundary marks the termination of many of the smaller and more gracile dinosaurs as well as their robust relatives. Conversely, turtles, crocodilians, and other survivors include some very large taxa. Perhaps the traumatic climatic/environmental shifts that marked the end of the Cretaceous, and had a direct and detrimental affect on vegetation, also had severe impacts on large herbivorous tetrapods. In turn, the devastation of the herbivorous megafauna could have had reverberations that affected all dinosaurs, including smaller predaceous forms. On the other hand, periods of climatic deterioration may not necessarily lead to

such a cascade of events; vegetation changes might even favor large herbivores, depending on the nature of the succeeding flora (Wing & Sues, 1992). The environmental changes caused by a single event, such as a bolide impact, would have to be sudden and intense in order to have such sweeping effects over a range of taxa and trophic levels. Still, the logical argument that such events were catastrophic and sudden sits oddly with a fossil record that shows the persistence of so many terrestrial groups across the K/T boundary.

EMERGENCE OF THE TERTIARY TERRESTRIAL MEGAFAUNA

The mosaic of extinction and survival that marked the Cretaceous-Tertiary transition has a quality that does suggest reorganization of the ecosystem. Dinosaurs represented most of the large terrestrial vertebrates during the Mesozoic, and their disappearance left a vacuum of size and trophic types that was not filled for a remarkably long time. Despite the rapid diversification of mammal taxa (Archibald, 1983) and the extraordinary increase in the size of many lineages (Alroy, 1998) during the Paleocene, mammals did not match the ecological range or the average body size of a herbivorous megafauna represented by the dinosaurs. For example, it has been noted that from the beginning of the Paleocene until the mid Cenozoic there were no high-browsing herbivores. Such forms, above 2 m in height, did not appear before the Oligocene, leaving a trophic gap of some 30 million years (see also comments in Wing & Sues, 1992). The influence of large browsing herbivores is evident in terms of their less discriminating feeding habits and greater potential alteration of the habitat (Peters, 1983; Crawley, 1983). Such a trophic impact could easily favor thorns, compensatory growth, and chemicals for defense of the assaulted vegetation. The coevolutionary relationships between the flora and the herbivorous megafauna may have set in motion conditions that stimulated the spread of grasslands and savannas in ways that augmented the effects of climate change in the Oligocene and later. This pattern of interdependence and ecosystem modification echoes that proposed for the radiations of browsing herbivorous dinosaurs and angiosperm-dominated flora in the Cretaceous. Authors (e.g., Webb & Opdyke, 1995) have also strongly emphasized the close relationship between climatic change, ecosystem disruption, and rapid pulses of turnover in the Cenozoic mammal fauna.

There remains the whole question of opportunity for diversification of both taxa and their adaptations

in the wake of the K/T extinction event. It is most popular here to suggest that the empty adaptive zones at the beginning of the Paleocene afforded such opportunities (Van Valen, 1978; Erwin et al., 1987). The emergence of many mammalian lineages with dentitions specialized for granivory and frugivory presumably opened up a great range of food sources and in turn provided a relatively new means of vertebrate-mediated dispersal of seeds and fruits so critical today in tropical rainforests (Tiffney, 1986). Still it is important to emphasize that during much of the Paleocene these explosive radiations were represented by mammals of comparatively small size. Indeed the diversity of dental, cranial, and skeletal specializations in Cretaceous mammals has been underemphasized, as have the potential adaptive opportunities for these creatures in Mesozoic terrestrial ecosystems. The easiest adaptive opportunity to characterize, namely, that for large, browsing herbivores, remained vacant for an appreciable period of some millions of years after the end of the Cretaceous, and persistently vacant for the largest body sizes. If these adaptive opportunities, these empty adaptive zones, were so readily available, why were their occupants so long in coming? The reasons for this lag in exploitation, as well as explanations for many other fascinating patterns that characterize the Cretaceous-Tertiary transition, remain elusive.

Literature Cited

- Agosti, D., D. A. Grimaldi & J. M. Carpenter. 1998. The oldest known ants. *Nature* 391: 447.
- Alifanov, V. R. 1989. The most ancient gecko (*Lacertilia*, Gekkonidae) from the Lower Cretaceous of Mongolia. *Paleontol. J. (Moscow)* 1: 124–126.
- Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science* 280: 731–734.
- Alvarez, W., F. Asharo, H. V. Michel & L. W. Alvarez. 1982. Iridium anomaly approximately synchronous with terminal Eocene extinctions. *Science* 216: 886–888.
- & F. Asaro. 1990. An extraterrestrial impact. *Sci. Amer.* 263: 78–84.
- Archer, M., T. F. Flannery, A. Ritchie & R. E. Molnar. 1985. First Mesozoic mammals from Australia—An Early Cretaceous monotreme. *Nature* 318: 363–366.
- Archibald, J. D. 1977. Fossil Mammalia and Testudines of the Hell Creek Formation, and the Geology of the Tullock and Hell Creek Formations. Ph.D. Dissertation, University of California, Berkeley.
- . 1983. Structure of the K-T mammal radiation in North America: Speculations on turnover rates and trophic structure. *Acta Palaeontol. Polon.* 28: 7–17.
- . 1996a. Dinosaur Extinction and the End of an Era. What the Fossils Say. Columbia Univ. Press, New York.
- . 1996b. Fossil evidence for a Late Cretaceous origin of "hoofed" mammals. *Science* 272: 1150–1153.

- & W. A. Clemens. 1982. Late Cretaceous extinctions. *Amer. Sci.* 70: 377–385.
- & L. Bryant. 1990. Differential Cretaceous-Tertiary extinctions of nonmarine vertebrates: Evidence from northeastern Montana. Pp. 549–62 in V. L. Sharpton & P. Ward (editors), *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. Special Pap. Geol. Soc. Amer., Vol. 247.
- Askin, R. A. 1988. The palynological record across the Cretaceous/Tertiary transition on Seymour Island, Antarctica. Pp. 155–62 in R. M. Feldman & M. O. Woodburne (editors), *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. Mem. Geol. Soc. Amer., Vol. 169.
- & R. A. Spicer. 1995. The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern latitudes: A comparison. Pp. 156–173 in *Effects of Past Global Change on Life*. Board on Earth Sciences and Resources, Commission on Geosciences, Environment, and Resources, National Resource Council.
- Axelrod, D. I. & P. H. Raven. 1978. Late Cretaceous and Tertiary vegetation history of Africa. Pp. 77–130 in M. J. A. Werger & A. C. Van Bruggen (editors), *Biogeography and Ecology of Southern Africa*. Dr. W. Junk, The Hague.
- Bakker, R. T. 1978. Dinosaur feeding behaviour and the origin of flowering plants. *Nature* 274: 661–663.
- Beard, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. Pp. 5–39 in K. C. Beard & M. R. Dawson (editors), *The Dawn of the Age of Mammals in Asia*. Bull. Carnegie Mus. Nat. Hist. 34.
- Benton, M. J. 1993. Reptilia. Pp. 681–715 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Bonaparte, J. F. 1987. History of the terrestrial Cretaceous vertebrates of Gondwana. *Actas IV Congr. Argentino Paleontol. y Bioestratigrafia, Mendoza 2*: 63–95.
- . 1990. New Late Cretaceous mammals from the Los Alamos Formation, Northern Patagonia. *Natl. Geogr. Res.* 6: 63–93.
- Borsuk-Bialynicka, M. 1991. Cretaceous lizard occurrences in Mongolia. *Cretaceous Res.* 12: 607–608.
- Brenner, G. J. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Pp. 23–47 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- Brinkman, D. & E. L. Nicholls. 1993. New specimen of *Bailemys praeclara* Hay and its bearing on the relationships of the Nanhsiungchelydidae (Reptilia: Testudines). *J. Paleontol.* 67: 1027–1031.
- Bryant, L. J. 1989. Non-dinosaurian lower vertebrates across the Cretaceous-Tertiary boundary in northeastern Montana. *Univ. Calif. Publ. Geol. Sci.* 134: 1–107.
- Burchardt, B. 1978. Oxygen isotope paleotemperatures from the Tertiary Period of the North Sea area. *Nature* 275: 121–123.
- Campbell, I. H., G. K. Czamanske, V. A. Fedorenko, R. I. Hill & V. Stepanov. 1992. Synchronism of the Siberian Traps and the Permian-Triassic boundary. *Science* 258: 1760–1763.
- Cappetta, H., C. Duffin & J. Zidek. 1993. Chondrichthyes. Pp. 592–619 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Chatterjee, S. 1989. The oldest Antarctic bird. *J. Vertebrate Paleontol.* 9(3): 16A.
- Chiappe, L. M. 1992. Enantiornithine (Aves) tarsometatarsi and the avian affinities of the Late Cretaceous Avosauridae. *J. Vertebrate Paleontol.* 12: 344–350.
- . 1995. The first 85 million years of avian evolution. *Nature* 378: 349–355.
- , M. A. Norell & J. M. Clark. 1998. A skull of a relative of the stem group bird *Mononykus*. *Nature* 392: 275–278.
- Cifelli, R. L. 1990. Cretaceous mammals of southern Utah: I. Marsupials from the Kaiparowits Formation (Judithian). *J. Vertebrate Paleontol.* 10: 295–319.
- . 1993a. Theria of metatherian-eutherian grade and the origin of marsupials. Pp. 205–215 in F. S. Szalay, M. J. Novacek & M. C. McKenna (editors), *Mammal Phylogeny, Vol. I: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*. Springer-Verlag, New York.
- . 1993b. Early Cretaceous mammal from North America and the evolution of marsupial dental characters. *Proc. Natl. Acad. U.S.A.* 90: 9413–9416.
- & R. L. Nydam. 1995. Primitive, helodermatid-like platynotan from the Early Cretaceous of Utah. *Herpetologica* 51(3): 286–291.
- Clemens, W. A. 1966. Fossil mammals of the type Lance Formation, Wyoming, Part II. Marsupialia. *Univ. Calif. Publ. Geol. Sci.* 62: 1–122.
- . 1973. Fossil mammals of the type Lance Formation, Wyoming, Part III. Eutheria and Summary. *Univ. Calif. Publ. Geol. Sci.* 94: 1–102.
- & Z. Kielan-Jaworowska. 1979. *Multituberculata*. Pp. 99–149 in J. A. Lillegraven, Z. Kielan-Jaworowska & W. A. Clemens (editors), *Mesozoic Mammals: The First Two-thirds of Mammal Evolution*. Univ. California Press, Berkeley, California.
- Collinson, M. E. & J. J. Hooker. 1987. Vegetational and mammalian faunal changes in the Early Tertiary of southern England. Pp. 259–304 in E. M. Friis, W. G. Chaloner & P. R. Crane (editors), *The Origins of Angiosperms and Their Biological Consequences*. Cambridge Univ. Press, New York.
- Coombs, Jr., W. P. 1978. The families of the ornithischian dinosaur order Ankylosauria. *Palaeontology* 21: 143–70.
- Cooper, A. & D. Penny. 1997. Mass survival of birds across the Cretaceous-Tertiary boundary: Molecular evidence. *Science* 275: 1109–1113.
- Courtillot, V. E. 1990. A volcanic eruption. *Sci. Amer.* 263: 85–92.
- Crabtree, D. R. 1987. Angiosperms of the northern Rocky Mountains: Albion to Campanian (Cretaceous) megafossil floras. *Ann. Missouri Bot. Gard.* 74: 707–747.
- Crane, P. R. & S. Lidgard. 1990. Angiosperm radiation and patterns of Cretaceous palynological diversity. Pp. 377–407 in P. D. Taylor & G. P. Larwood (editors), *Major Evolutionary Radiations*. Syst. Assoc. Spec. Vol. 42.
- , S. R. Manchester & D. L. Dilcher. 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. *Fieldiana, n.s.* 20: 1–63.
- Crawley, M. J. 1983. *Herbivory: The Dynamics of Plant-Animal Interactions*. Univ. California Press, Berkeley.
- Crepet, W. L. & E. M. Friis. 1987. The evolution of insect pollination in angiosperms. Pp. 181–201 in E. M. Friis, W. G. Chaloner & P. R. Crane (editors), *The Origins of*

- Angiosperms and Their Biological Consequences. Cambridge Univ. Press, New York.
- Currie, P. J. & K. Padian (editors). 1997. Encyclopedia of Dinosaurs. Academic Press, San Diego.
- D'Hondt, S., H. Sigurdsson, A. Hanson, S. Carey & M. Pilson. 1994. Sulfate volatilization, surface-water acidification, and extinction at the KT boundary. New developments regarding the KT event and other catastrophes in earth history. *Lunar Planet. Inst. Contr.* 825: 29–30.
- Dashzeveg, D., M. J. Novacek, M. A. Norell, J. M. Clark, L. M. Chiappe, A. Davidson, M. C. McKenna, L. Dingus, C. Swisher & P. Altangerel. 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. *Nature* 374: 446–449.
- Drinnan, A. N. & P. R. Crane. 1990. Cretaceous paleobotany and its bearing on the biogeography of austral angiosperms. Pp. 192–219 in T. N. Taylor & E. L. Taylor (editors), *Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana*. Springer-Verlag, New York.
- , ———, E. M. Friis & K. R. Pedersen. 1990. Lauraceous flowers from the Potomac Group (mid-Cretaceous) of eastern North America. *Bot. Gaz. (Crawfordsville)* 151: 370–384.
- Elzanowski, A. 1995. Cretaceous birds and avian phylogeny. *Courier Forschungsinst. Senckenberg* 181: 37–53.
- Erwin, D. H., J. W. Valentine & J. J. Sepkoski, Jr. 1987. A comparative study of diversification events: The early Paleozoic versus the Mesozoic. *Evolution* 41: 1176–1186.
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation eastern Wyoming. *Univ. Calif. Publ. Geol. Sci.* 49: 1–187.
- . 1969. A new fossil discoglossid frog from Montana and Wyoming. *Breviora* 328: 1–7.
- . 1982. Systematics and paleogeography of some fossil salamanders and frogs. *Natl. Geogr. Soc. Res. Rep.* 14: 191–210.
- . 1983. The fossil record and early distribution of lizards. Pp. 365–398 in A. G. J. Rhodin & K. Kiyata (editors), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams*. Museum of Comparative Zoology, Harvard Univ., Cambridge, Massachusetts.
- , K. De Queiroz & J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pp. 119–281 in R. Estes & G. Pregill (editors), *Phylogenetic Relationships within Squamata*. Stanford Univ. Press, Stanford, California.
- Fastovsky, D. E. & K. McSweeney. 1987. Paleosols spanning the Cretaceous-Paleogene transition, eastern Montana and western North Dakota. *Palaos* 2: 282–295.
- Feduccia, A. 1995. Explosive evolution in Tertiary birds and mammals. *Science* 267: 637–638.
- & R. Wild. 1993. Birdlike characters in the Triassic archosaur *Megalancosaurus*. *Naturwissenschaften* 80: 564–566.
- Flynn, J. J. 1986. Faunal provinces and the Simpson coefficient. Pp. 317–338 in K. M. Flanagan & J. A. Lillegraven (editors), *Vertebrates, Phylogeny, and Philosophy*. Contr. Geol. Univ. Wyoming Spec. Pap. 3.
- Fox, R. C. 1984. *Paranyctoides maleficus* (new species), an early eutherian mammal from the Cretaceous of Alberta. *Carnegie Mus. Nat. Hist. Spec. Publ.* 9: 9–20.
- Friis, E. M. & W. L. Crepet. 1987. Time of appearance of floral features. Pp. 145–179 in E. M. Friis, W. G. Chaloner & P. R. Crane (editors), *The Origins of Angiosperms and Their Biological Consequences*. Cambridge Univ. Press, New York.
- , K. R. Pederson & P. R. Crane. 1999. Early angiosperm diversification: The diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. *Ann. Missouri Bot. Gard.* 86: 259–296.
- Gaffney, E. S. & P. A. Meylan. 1988. A phylogeny of turtles. Pp. 157–219 in M. J. Benton (editor), *The Phylogeny and Classification of the Tetrapods*, Vol. 1. Amphibians, Reptiles, Birds. Clarendon Press, Oxford.
- Gao, K. 1994. First discovery of Late Cretaceous cordylids (Squamata) from Madagascar. *J. Vertebrate Paleontol.* 14: 26A, Suppl. 3. Abstracts of Papers, 54th Annual meetings, Society of Vertebrate Paleontology, Burke Museum, Univ. Washington, Seattle, Washington.
- & R. C. Fox. 1996. Taxonomy and Evolution of Late Cretaceous Lizards (Reptilia: Squamata) from Western Canada. *Bull. Carnegie Mus. Nat. Hist.* 33.
- & L. Hou. 1995. Iguanians from the Upper Cretaceous Djadochta Formation, Gobi Desert, China. *J. Vertebrate Paleontol.* 15: 57–78.
- Gardiner, B. G. 1993. Osteichthyes: Basal Actinopterygians. Pp. 611–619 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. Pp. 1–55 in K. Padian (editor), *The Origin of Birds and the Evolution of Flight*, Vol. 8. Mem. Calif. Acad. Sci.
- , R. Estes & K. De Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15–98 in R. Estes & G. Pregill (editors), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford Univ. Press, Stanford.
- Gradzinski, R., Z. Kielan-Jaworowska & T. Maryánská. 1977. Upper Cretaceous Djadochta, Barun Goyot, and Nemegt Formations of Mongolia, including remarks on previous subdivisions. *Acta Geol. Polon.* 27: 281–318.
- Gregory, W. K. & G. G. Simpson. 1926. Cretaceous mammal skulls from Mongolia. *Amer. Mus. Novit.* 225: 1–20.
- Grieve, R. A. F. & P. B. Robertson. 1987. Terrestrial impact structures. *Geol. Surv. Canada, Map* 1658A.
- Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann. Missouri Bot. Gard.* 86: 373–406.
- Hansen, H. J. 1991. Diachronous disappearance of marine and terrestrial biota at the Cretaceous-Tertiary boundary. Pp. 31–32 in Z. Kielan-Jaworowska, N. Heintz & H. A. Nakrem (editors), *Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota (extended abstracts)*, Vol. 364. Contr. Paleontol. Museum, Univ. Oslo.
- Hedges, S. B., P. H. Parker, C. G. Sibley & S. Kumar. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature* 381: 226–229.
- Hennig, W. 1981. *Insect Phylogeny*. John Wiley & Sons, Chichester.
- Hildebrand, A. R., M. Pilkington, M. Connors, C. Oritz-Aleman & R. E. Chavez. 1995. Size and structure of the Chicxulub crater revealed by horizontal gravity gradients and cenotes. *Nature* 376: 415–417.
- Hill, R. S. 1982. The Eocene megafossil flora of Nerriga, New South Wales, Australia. *Palaeontographica B* 181: 44–77.
- Hooker, J. J. 1992. An additional record of a placental mammal (Order Astrapotheria) from the Eocene of West Antarctica. *Antarct. Sci.* 4: 107–108.

- Hou L. & Z. Liu. 1984. A new fossil bird from Lower Cretaceous of Gansu and early evolution of birds. *Scientia Sinica (Ser. B)* 27(12): 1296–1302.
- Hutchison, J. H. & J. D. Archibald. 1986. Diversity of turtles across the Cretaceous/Tertiary boundary in northeastern Montana. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 55: 1–22.
- Izett, G. A., W. A. Cobban, J. D. Obradovich & M. J. Kunk. 1993. The Manson impact crater structure: $^{40}\text{Ar}/^{39}\text{Ar}$ age and its distal impact ejecta in the Pierre Shale in southeastern South Dakota. *Science* 262: 729–732.
- Janis, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Rev. Ecol. Syst.* 24: 467–500.
- Jerzykiewicz, T., P. J. Currie, D. A. Eberth, P. A. Johnston, E. H. Koster & J.-J. Zheng. 1993. Djadokhta Formation correlative strata in Chinese inner Mongolia: An overview of the stratigraphy sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Canad. J. Earth Sci.* 30: 2180–2195.
- Johnson, K. R., D. J. Nichols, M. Attrep, Jr. & C. J. Orth. 1989. High-resolution leaf-fossil record spanning the Cretaceous/Tertiary boundary. *Nature* 340: 708–711.
- & L. J. Hickey. 1991. Megafloreal change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, USA. Pp. 433–44 in V. L. Sharpton & P. D. Ward (editors), *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. Special Pap. Geol. Soc. Amer. 247: 433–444.
- Kielan-Jaworowska, Z. 1974. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). *Palaeontologia Polonica* 30: 25–44.
- . 1992. Interrelationships of Mesozoic mammals. *Hist. Biol.* 6: 185–201.
- & D. Dashzeveg. 1989. Eutherian mammals from the Early Cretaceous of Mongolia. *Zool. Ser.* 18: 347–355.
- Krause, D. W., G. V. R. Prasad, W. Von Koenigswald, A. Sahni & F. E. Grine et al. 1997. Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature* 390: 504–507.
- Kumar, S. & S. B. Hedges. 1998. A molecular timescale for vertebrate evolution. *Nature* 392: 917–919.
- Kurochkin, E. N. 1988. Fossil reptiles and birds from Mongolia. *Trans. Joint Soviet-Mongolian Paleontol. Exped.* 34: 33–42.
- Lehman, T. M. 1990. Paleosols and the Cretaceous/Tertiary transition in the Big Bend region of Texas. *Geology* 18: 362–64.
- Lidgard, S. & P. R. Crane. 1990. Angiosperm diversification and Cretaceous floristic trends: A comparison of palynofloras and leaf macrofloras. *Paleobiology* 16: 77–93.
- Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *Univ. Kansas Paleontol. Contr. Art.* 50, *Vertebrates* 12: 1–122.
- & M. C. McKenna. 1986. Fossil mammals from the “Mesaverde” Formation (Late Cretaceous, Judithian) of the Bighorn and Wind River basins, Wyoming, with definitions of the Late Cretaceous North American Land-Mammal “Ages.” *Amer. Mus. Novit.* 2840: 1–68.
- Loope, D. B., L. Dingus, C. C. Swisher, III & C. Minjin. 1998. Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia. *Geology* 26: 27–30.
- Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. *Ann. Missouri Bot. Gard.* 86: 472–522.
- Marshall, L. G. & R. L. Cifelli. 1990. Analysis of changing diversity patterns in Cenozoic land mammal age faunas, South America. *Palaeovertebrata* 19: 169–210.
- Martin, L. D. 1991. Mesozoic birds and the origin of birds. Pp. 485–550 in H.-P. Schultze & L. Trueb (editors), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell Univ. Press, Ithaca.
- Maryánská, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologia Polonica* 37: 85–151.
- & H. Osmólska. 1974. Pachycephalosauria, a new suborder of ornithischian dinosaurs. *Palaeontologia Polonica* 30: 45–102.
- & ———. 1975. Results of the Polish-Mongolian Palaeontological Expedition, Part VI. Protoceratopsidae (Dinosauria) of Asia. *Palaentol. Polon.* 33: 133–182.
- McKenna, M. C. 1983. Holocene landmass rearrangement, cosmic events, and Cenozoic terrestrial organism. *Ann. Missouri Bot. Gard.* 70: 459–489.
- & S. K. Bell. 1997. *Classification of Mammals above the Species Level*. Columbia Univ. Press, New York.
- Michener, C. D. & D. A. Grimaldi. 1988. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proc. Natl. Acad. U.S.A.* 85: 6424–6426.
- Miller, K. G. 1992. Middle Eocene to Oligocene stable isotopes, climate, and deep-water history: The Terminal Eocene Event? Pp. 160–177 in D. R. Prothero & W. A. Berggren (editors), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton Univ. Press, Princeton.
- Milner, A. R. 1993. Amphibian-grade Tetrapoda. Pp. 665–679 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Moyle, P. B. & J. J. Cech, Jr. 1988. *Fishes: An Introduction to Ichthyology*. Prentice Hall, Englewood Cliffs, New Jersey.
- Nessov, L. A. 1985. Rare bony fishes, terrestrial lizards and mammals from the lagoonal zone of the littoral lowlands of the Cretaceous of the Kyzylkumy. *Year-Book of All-Union Palaeontol. Soc., Leningrad* 28: 199–219. [In Russian.]
- . 1988. Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta Zool. Cracoviensia* 31: 475–486.
- & A. A. Jarkov. 1989. New Cretaceous-Paleocene birds of the USSR and some remarks on the origin and evolution of the Class Aves. *Proc. Zool. Inst., USSR Acad. Sci.* 197: 78–97. [In Russian.]
- & ———. 1992. Review of the localities and remains of Mesozoic and Paleogene birds of the USSR and the description of new findings. *Russian J. Ornith.* 1(1): 7–50. [In Russian.]
- Newsom, H. E., G. Graup, D. A. Iseri, J. W. Geissman & K. Keil. 1990. The formation of the Ries Crater, West Germany: Evidence of atmospheric interactions during a large cratering event. Pp. 195–206 in V. L. Sharpton & P. Ward (editors), *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. Special Pap. Geol. Soc. Amer., Vol. 247.
- Nichols, D. J., D. M. Jarzen, C. J. Orth & P. Q. Oliver. 1986. Palynological and iridium anomalies at Cretaceous-Tertiary boundary, south-central Saskatchewan. *Science* 231: 714–717.

- Norell, M. A. 1992. Taxic origin and temporal diversity: The effect of phylogeny. Pp. 89–118 in M. J. Novacek & Q. D. Wheeler (editors), *Extinction and Phylogeny*. Columbia Univ. Press, New York.
- & M. J. Novacek. 1992. The fossil record and evolution: Comparing cladistic and paleontologic evidence for vertebrate history. *Science* 255: 1690–1693.
- Noriega, J. & C. Tambussi. 1995. A late Cretaceous Presbyornithidae (Aves: Anseriformes) from Vega Island, Antarctic Peninsula: Paleobiogeographic implications. *Ameghiniana* 32: 57–61.
- Novacek, M. J. 1996. *Dinosaurs of the Flaming Cliffs*. Anchor/Doubleday, New York.
- . 1997. Mammalian evolution: An early record bristling with evidence. *Curr. Biol.* 7: R489–R491.
- , M. A. Norell, M. C. McKenna & J. Clark. 1994. Fossils of the Flaming Cliffs. *Sci. Amer.* 271: 60–69.
- , G. W. Rougier, J. R. Wible, M. C. McKenna, D. Dashzeveg & I. Horovitz. 1997. Epipubic bones in eutherian mammals from the Late Cretaceous of Mongolia. *Nature* 389: 483–486.
- Olson, S. L. 1985. The fossil record of birds. Pp. 79–238 in D. S. Farner, J. R. King & K. C. Parkes (editors), *Avian Biology*, Vol. 8. Academic Press, New York.
- . 1992. *Neogaeornis wetzeli* Lambrecht, a Cretaceous loon from Chile (Aves: Gaviidae). *J. Vertebrate Paleontol.* 12(1): 122–124.
- Orth, C. J., J. S. Gilmore, J. D. Knight, C. L. Pillmore, R. H. Tschudy & J. E. Fassett. 1981. An iridium abundance anomaly at the palynological Cretaceous-Tertiary boundary in northern New Mexico. *Science* 214: 1341–1342.
- Padian, K. & L. M. Chiappe. 1998a. The origin of birds and their flight. *Sci. Amer.* 278(2): 38–47.
- & ———. 1998b. The origin and early evolution of birds. *Biol. Rev.* 73: 1–42.
- Parker, L. R. 1976. The paleocology of the fluvial coal-forming swamps and associated floodplain environments in the Blackhawk Formation (Upper Cretaceous) of central Utah. Pp. 99–166 in A. T. Cross & E. B. Maxfield (editors), *Aspects of Coal Geology, Northwest Colorado Plateau: Some Geologic Aspects of Coal Accumulation, Alteration, and Mining in Western North America*. Brigham Young Univ. Geol. Stud., Vol. 22.
- Parrish, J. T. & R. A. Spicer. 1988. Middle Cretaceous wood from the Nanushuk Group, central North Slope Alaska. *Palaeontology* 31: 19–34.
- Patterson, C. 1993. Osteichthyes: Teleostei. Pp. 621–656 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge Univ. Press, Cambridge.
- Pillmore, C. L., M. G. Lockley, R. F. Fleming & K. R. Johnson. 1994. Footprints in the rocks: New evidence from Raton Basin that dinosaurs flourished on land until the terminal Cretaceous impact event. New developments regarding the KT event and other catastrophes in earth history. *Lunar and Planetary Inst. Contr.* 825: 90.
- Pirrie, D. & J. D. Marshall. 1990. High-latitude Late Cretaceous paleotemperatures: New data from James Ross Island, Antarctica. *Geology* 18: 31–34.
- Prasad, G. V. R., J. J. Jaegar, A. Sahni, E. Gheerbrant & C. K. Khajuria. 1994. Eutherian mammals from the Upper Cretaceous (Maastrichtian) intertrappean beds of Naskal, Andhra Pradesh, India. *J. Vertebrate Paleontol.* 14: 260–277.
- Prothero, D. R. 1985. North American mammalian diversity and Eocene-Oligocene extinctions. *Paleobiology* 11: 389–405.
- & W. A. Berggren (Editors). 1992. *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton Univ. Press, Princeton.
- Raine, J. I. 1988. The Cretaceous/Cainozoic boundary in New Zealand terrestrial sequences. Abstracts of the Seventh International Palynological Congress, Brisbane 137.
- Raup, D. M. 1991. *Extinction: Bad Genes or Bad Luck?* W. W. Norton, New York.
- Retallack, G. J., G. D. Leahy & M. D. Spoon. 1987. Evidence from paleosols for ecosystem changes across the Cretaceous/Tertiary boundary in eastern Montana. *Geology* 15: 1090–1093.
- Rich, T. H., P. Vickers-Rich, A. Constantine, T. F. Flannery, L. Kool & N. Van Klaveren. 1997. A tribosphenic mammal from the Mesozoic of Australia. *Science* 278: 1438–1442.
- Richter, A. 1994. Lacertilia aus der Unteren Kreide um Uña und Galva (Spanien) und Anoual (Marokko). *Berliner Geowissenschaftliche Abh., Reihe E, Band 14*: 1–138.
- Romero, E. J. 1986. Paleogene phytogeography and climatology of South America. *Ann. Missouri Bot. Gard.* 73: 449–461.
- Rose, K. D. 1981. Composition and species diversity in Paleocene and Eocene mammal assemblages: An empirical study. *J. Vertebrate Paleontol.* 1: 367–388.
- . 1984. Evolution and radiation of mammals in the Eocene, and the diversification of modern orders. Pp. 110–127 in P. D. Gingerich & C. E. Badgley (editors), *Mammals: Notes for a Short Course*. Univ. Tennessee, Dept. Geol. Studies in Geol. 8.
- Rougier, G. W. & M. J. Novacek. 1998. Early mammals: Teeth, jaws, and finally . . . a skeleton! *Curr. Biol.* 8: R284–R287.
- , J. R. Wible & M. J. Novacek. 1996. Middle-ear ossicles of the multituberculate *Kryptobaatar* from the Mongolian Late Cretaceous: Implications for mammalian relationships and the evolution of the auditory apparatus. *Amer. Mus. Novit.* 3187: 1–43.
- , M. J. Novacek & D. Dashzeveg. 1997. A new multituberculate from the Late Cretaceous Locality Ukhaa Tolgod, Mongolia. Considerations on multituberculate interrelationships. *Amer. Mus. Novit.* 3191: 1–26.
- , J. R. Wible & M. J. Novacek. 1998. Implications of *Deltatheridium* specimens for early marsupial history. *Nature* 396: 459–371.
- Russell, D. A. 1970. A skeletal reconstruction of *Leptoceraptops gracilis* from the upper Edmonton Formation. *Canad. J. Earth Sci.* 7: 181–184.
- . 1984. The gradual decline of the dinosaurs—Fact or fallacy? *Nature* 307: 360–361.
- Saito, T., T. Yamanoi & K. Kaiho. 1986. Devastation of the terrestrial flora at the end of the Cretaceous in the Boreal Far East. *Nature* 323: 253–256.
- Sanz, J. L., L. M. Chiappe, B. P. Perez-Moreno, J. J. Moratalla, F. Hernandez-Carrasquilla, A. D. Buscalioni, F. Ortega, F. J. Poyato-Ariza, D. Rasskin-Gutman & X. Martinez-Delclos. 1997. A nestling bird from the Lower Cretaceous of Spain: Implications for avian skull and neck evolution. *Science* 276: 1543–1546.
- Savage, D. E. & D. E. Russell. 1983. *Mammalian Paleofaunas of the World*. Addison-Wesley, Massachusetts.
- Scotese, C. R. 1997. *Paleogeographic Atlas, PALEOMAP*

- progress report 90-0497, pp. 1-45. Department of Geology, Univ. Texas at Arlington, Arlington, Texas.
- Seiffert, J. 1973. Upper Jurassic lizards from central Portugal. *Serv. Geol. de Portugal, Separata da Mem.* 22: 1-85.
- Sereno, P. C. 1997. The origin and evolution of dinosaurs. *Annual Rev. Earth Planet. Sci.* 25: 435-489.
- Sheehan, P. M., D. E. Fastovsky, R. G. Hoffman, C. B. Berghaus & D. L. Gabriel. 1991. Sudden extinction of the dinosaurs: Latest Cretaceous, upper Great Plains, USA. *Science* 254: 835-839.
- Shultze, H.-P. 1993. Osteichthyes: Sarcopterygii. Pp. 657-663 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Smith, A. B. & C. H. Jeffery. 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous Period. *Nature* 392: 69-71.
- Smith, A. G., D. G. Smith & B. M. Funnell. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge Univ. Press, Cambridge.
- Spicer, R. A. & J. T. Parrish. 1986. Paleobotanical evidence for cool north polar climates in middle Cretaceous (Albian-Cenomanian) time. *Geology* 14: 703-706.
- Stets, J., A. R. Ashraf, H. K. Erben, G. Hahn, U. Hambach, K. Krumsiek, J. Thein & P. Wurster. 1995. The Cretaceous-Tertiary boundary in the Nanxiong Basin (continental facies, southeast China). Pp. 349-371 in N. MacLeod & G. Keller (editors), *The Cretaceous-Tertiary Mass Extinction: Biotic and Environmental Effects*. W. W. Norton, New York.
- Stucky, R. K. 1990. Evolution of land mammal diversity in North America during the Cenozoic. Pp. 375-432 in H. H. Genoways (editor), *Current Mammalogy*, Vol. 2. Plenum Press, New York.
- & M. C. McKenna. 1993. Mammalia. Pp. 739-771 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Sues, H. D. & P. M. Galton. 1987. Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). *Palaeontographica, A* 198: 1-40.
- Sullivan, R. M. 1987. A reassessment of reptilian diversity across the Cretaceous-Tertiary Boundary. *Contr. Sci. Nat. Hist. Mus. Los Angeles County* 391: 1-25.
- Swisher, C. C., III & D. R. Prothero. 1990. Single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Eocene-Oligocene transition in North America. *Science* 249: 760-762.
- Szalay, F. S. & M. C. McKenna. 1971. Beginning of the age of mammals in Asia: The late Paleocene Gashato Fauna, Mongolia. *Bull. Amer. Mus. Nat. Hist.* 144: 271-317.
- Tarsitano, S. 1991. *Archaeopteryx*: Quo Vadis? Pp. 541-576 in H. P. Schultze & L. Trueb (editors), *Origins of the Higher Groups of Tetrapods*. Cornell Univ. Press, Ithaca, New York.
- Tiffney, B. H. 1986. Evolution of seed dispersal syndromes according to the fossil record. Pp. 273-305 in D. R. Murray (editor), *Seed Dispersal*. North Ryde, N. S. W. Academic Press, Australia.
- Tokaryk, T. T. & P. C. James. 1989. *Cimolopteryx* sp. (Aves, Charadriiformes) from the Frenchman Formation (Maastrichtian), Saskatchewan. *Canad. J. Earth Sci.* 26(12): 2729-2730.
- Tschudy, R. H., C. L. Pillmore, C. J. Orth, J. S. Gilmore & J. D. Knight. 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous-Tertiary boundary, western Interior. *Science* 225: 1030-1032.
- & B. D. Tschudy. 1986. Extinction and survival of plant life following the Cretaceous-Tertiary boundary event, Western Interior, North America, lake, Morrison Formation, eastern Colorado Plateau. *Bull. Geol. Soc. Amer.* 103: 538-558.
- Unwin, D. 1993. Aves. Pp. 717-737 in M. J. Benton (editor), *The Fossil Record 2*. Chapman & Hall, London.
- Valen, L. Van. 1978. The beginning of the age of mammals. *Evol. Theory* 4: 45-80.
- Webb, S. D. 1977. A history of savanna vertebrates in the New World, Part 1. North America. *Annual Rev. Ecol. Syst.* 8: 355-380.
- & N. D. Opdyke. 1995. Global climatic influence on Cenozoic land mammal faunas. Pp. 184-208 in *Effects of Past Global Change on Life*. Board on Earth Sciences and Resources, Commission on Geosciences, Environment, and Resources, National Resource Council.
- Weishampel, D. B. 1990. Dinosaurian distribution. Pp. 63-139 in D. B. Weishampel, P. Dodson & H. Osmólska (editors), *The Dinosauria*. Univ. California Press, Berkeley.
- & D. B. Norman. 1989. Vertebrate herbivory in the Mesozoic: Jaws, plants, and evolutionary metrics. Pp. 87-100 in J. O. Farlow (editor), *Paleobiology of the Dinosauria*. Special Pap. Geol. Soc. Amer., Vol. 238.
- , P. Dodson & H. Osmólska (editors). 1990. *The Dinosauria*. Univ. California Press, Berkeley.
- Whalley, P. 1986. A review of current fossil evidence of Lepidoptera in the Mesozoic. *Biol. J. Linn. Soc.* 28: 253-71.
- Wilson, E. O. 1987. The earliest known ants: An analysis of the Cretaceous species and inference concerning their social organization. *Paleobiology* 13: 44-53.
- Wilson, M. V. H., D. B. Brinkman & A. G. Neuman. 1992. Cretaceous Escoidei (Teleostei): Early radiation of the pikes in North American fresh water. *J. Paleontol.* 66: 839-846.
- Wing, S. L. 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. *Ann. Missouri Bot. Gard.* 74: 748-784.
- & H. D. Sues. 1992. Mesozoic and Early Cenozoic terrestrial ecosystems. Pp. 327-416 in A. K. Behrensmeyer et al. (editors), *Terrestrial Ecosystems through Time*. Univ. Chicago Press, Chicago.
- & B. H. Tiffney. 1987. The reciprocal interaction of angiosperm evolution and tetrapod herbivory. *Rev. Palaeobot. Palynol.* 50: 179-210.
- Winkler, D. A., P. A. Murry & L. L. Jacobs. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *J. Vertebrate Paleontol.* 10: 95-116.
- Wolbach, W. S., I. Gilmour & E. Anders. 1990. Major wildfires at the Cretaceous/Tertiary boundary. Pp. 391-400 in V. L. Sharpton & P. Ward (editors), *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. Special Pap. Geol. Soc. Amer., Vol. 247.
- Wolfe, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *Amer. Sci.* 66: 694-703.
- . 1985. Distribution of major vegetational types during the Tertiary. *Geophysical Monogr.* 32: 357-375.
- . 1987. Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* 13: 215-226.

- & G. R. Upchurch, Jr. 1986. Vegetation, climatic, and floral changes at the Cretaceous-Tertiary boundary. *Nature* 324: 148–152.
- & ———. 1987. North American nonmarine climates and vegetation during the Late Cretaceous. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 61: 33–77.
- Woodburne, M. O. & C. C. Swisher, III. 1995. Land Mammal High-Resolution Geochronology, Intercontinental Overland Dispersals, Sea Level, Climate, and Vicariance. *Geochronology Time Scales and Global Stratigraphic Correlation*. SEPM Special Publ. 54: 335–364.
- & W. J. Zinsmeister. 1982. Fossil land mammal from Antarctica. *Science* 218: 284–286.
- Wueterich, B. 1997. Will fossil from down under upend mammal evolution? *Science* 278: 1401–1402.
- Ziegler, A. M., A. L. Raymond, T. C. Gierlowski, M. A. Horrell, D. B. Rowley & A. L. Lottes. 1987. Coal, climate, and terrestrial productivity: The present and early Cretaceous compared. Pp. 25–29 *in* A. C. Scott (editor), *Coal, and Coal-Bearing Strata: Recent Advances*. Special Pap. Geol. Soc. Amer., Vol. 32.